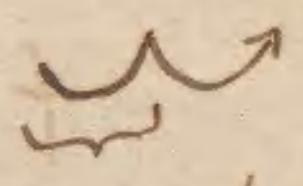


August 18th, 1955

Dear Martin,

Sorry for waiting so long with my reply; I hope there is not an already finished paper of yours lurking ~~somewhere~~ and just waiting for this gap to be filled.

Your description of the "ritual flight" of the Kittiwake is quite correct, except for one point: You say that the birds have their wings set and glide in the downphase and then beat the wings as they fly upwards. But beating and gliding do not alternate so regularly; a bird may fly one or more complete arches 
this I mean by one arch

without one single wing beat, or it may do so ~~beating~~ continuously, it may beat in the upphase only, or in the downphase only etc. I got the impression, that the birds start to beat at any phase of the performance whenever beating is required and that they continue to do so as long as it is necessary for keeping up speed, i.e. I don't think that there is a ritualized alternation of wing beating and gliding.

221. 11. 30. 1930

The flight is accompanied, as you say, by the moaning call, the same moan as in the arch-and-bow-



positive

usually

The performance indeed is ~~often~~ not directed straight

toward or away from a nearby flying bird, but the performer often flies after its opponent in a very loose

[! Ed.]

way. After a dispute on the ledges bird A may for instance fly away, bird B follows with the ritual flight, but after a few yards B deviates already from the path,

taken by A and continues ritual flying in a different

direction. The performance may also be ~~orientated in relation to~~ a

bird on the cliff: During a dispute on the ledges

A alone may fly away, describe a circle in the

ritual flight and land either on its own ledge

continuing the dispute, or try to land on B's ledge

in order to drive B off. (A may also shut up after

landing on its own ledge after such a flight and settle to a peaceful activity, B may leave while A is ritual flying,

particularly often he does so just as A is coming back towards the ledges, and in any other alternatives, as you know too well).

I have seen occasionally that the down phase ^{of the ritual flight} was directed straight at the opponent, leading to an attack or an attempt at least, but this, as far as I remember, is ~~very~~ ^{rather} rare, while the non-oriented form of the performance is very common indeed.

The motivation of the flight is obviously attack & presumably escape.

I think it is very nice that you get something similar in Franklin's full and I will of course be delighted to get quoted as personal communication.

I hope I have told you all you want to know.

I still have not started working out my field notes from either year in a systematic way. In the first winter the preparation of my thesis for print has held me up and last winter I had to shake a preliminary paper

out of my sleeve somehow, without having time to whip my notes into a useful system. But now the time has come (i.e. after the conference in Holland) when I will goad over them, probably for the next 2 years.

We have now finished on the Fans for good. More and more people have discovered that there is a "study centre" there and more and more # of them stream there ^{to stay} for a fortnight or so.

We don't know what we are going to do after Duke has finished his thesis, he thinks vaguely of doing some experimental work in the lab.

Yours Esther

regards from Duke.

6 February 57

Zoo Dept.

The abstract/paper
in the main conference
comes by sea mail.

Dear Martin,

Herewith, at last, another copy of the Grongigen stuff - for what good it may do you. I would be glad to have back the copy of the notes on the G & T conference after you have finished with them. There probably won't be many points of interest to you there I think, which you haven't heard before. The summaries of the conference talks you may keep if you want to.

Many thanks for your last letter, a very prompt reply to mine. Niko sent on the second part of the gull paper for Behaviour without showing it to anyone here - indeed without our even knowing it was here - which was rather maddening, but we shall see it soon. So I'm afraid I can't send any comments on it - nice or nasty!

In your last letter you ask me to avoid using the word food-begging to describe a certain display in the terns but you don't say why and I'm not sure if I understand. Is it because ~~it~~ you want a descriptive rather than a functional (or causal) name? I am rather reluctant to change what seems to me such a convenient name unless you have a very strong reason, but I get the impression from your language that you have.

I was very glad to get the information about the begging, sorry the "begging", of Gull-billed, Inca and Noddy Terns.

The Jensen paper is 1946, Dansk Orn. Foren. Tidskr. 40:80-96. (Danish with English summary).

I hope you will answer the question about the Upright Threat which you see in some terns, which I asked in my letter of 1 Aug 56. I am still at a loss to know whether this is a real difference between your spp and mine, or whether I am not recognising something which you call the upright threat. I realise that there is a real possibility of the second alternative for even in the gulls I suspect that you recognise it whereas others don't.

77:175-181
L

E.g. in winter D. Franck (Vogelwelt 1956) ~~saw~~ saw no sign of any upright in B-h Gs which he watched and Gilbert Manley, who is trying to follow on your work here on the B-h G, has also been watching them in London and can't see it. In addition Franck never saw Choking while Manley has seen it only once, in exactly the "right" circumstances when a very aggressive male was suddenly resisted by another. This choking business fits nicely with your interpretation, but the lack of uprights doesn't seem to fit unless they are completely overlooking them.

About the development of calls in gulls you will have seen Goethe's paper in the Z. Tierpsychol. on the Herring Gull. He seems to start from two calls and some of these develop into calls of the adults

but other calls appear apparently de novo. Do you think this is a real disagreement with your findings in the Franklin's and Ring-billed Gulls?

You remember the Ascension trip I told you about. I turned down the idea in its original form but have accepted instead the idea of going there for 3 months next winter (our winter), partly to give the other people ^{the full time} ~~some~~ idea of what kind of studies one can make in the field and partly to do something myself. You wrote that you intended to make a thorough study of the Noddies, the Fairy Tern and Ternlets. From what I know of your "methods" I presume that you confine yourself to displays and won't be making a ~~good~~ study of the general breeding behaviour. Is this correct? On the assumption that it is I think there will be plenty more which one can do with the terns there (Sooty, 2 Noddies, and Fairy Tern). One idea I am keen to work on is a comparison of the two Noddies to see whether the apparent nest-site differences can be correlated with other differences in behaviour. I would also like to do some work on the incubation and parental behaviour with experiments on egg and young recognition which I think can be done with ~~more~~ a different viewpoint than before. Naturally I shall also look at the displays to see how they compare with the species I know, but I realise that you are probably able to go much farther with this ~~than~~ I can, on the basis of your wider comparative studies. I shall look forward for example to seeing the aerial display, ~~xxxxx~~ especially the High Flight, to see what happens there. - If there is one. Of the other people on the expedition one hopes to work on the general problem of the seasonal periodicity of the Sooties and the other will perhaps have a look at Gygis. Neither is madly interested in behaviour in the narrow sense so I don't think they should conflict very much with your work, but I should like it, all the same, if you were able to let us have a scheme of the sort of things which you have covered. You might at the same time tell me the sort of things which you ~~might~~ like to have more information about than, perhaps, you were able to get in the time. ~~All~~ ~~xx~~ my plans turn, of course, on when the birds will breed. Oct/Nov seems likely for the Sooties and the rest probably Nov. ~~xx~~ So I can't make up my mind too definitely in advance. If no bird breeds during my stay I shall have to turn to land-crabs!

Thanks for the information about tern systematics. I wonder where Chlidonias fits in your scheme and do you include Phaetusa with Sterna? or is the scheme deliberately incomplete? I have been puzzling about the question of forked tails for a time and it seems to me that they might well develop independently in more or less square-tailed birds which take to feeding by flying slowly, close to the speed of stalling (as Sterna does), over the water as it searches beneath itself for prey. Indeed one might expect

xxxx forking to be correlated with a change from the scavenging habits on the ground of gulls to this quite different kind of hunting for fish or water-insects. Does this seem reasonable to you ? On these sorts of grounds I feel that the terns could be polyphyletic (as you suggestx) whether in fact they are or not.

By the way I don't think I have mentioned about the work that the two new fellows are to do at Ravenglass on the B-h G. One, as I have said, hopes to try and find out more about the causation and function of the various displays using models and mirrors, ~~the other~~ and also to try and find out more about the variations in the normal form of the displays. The other man, a New Zealander, Colin Beer, will study parental behaviour extending Rita's work on egg acceptance at beginning and end of the season, brooding behaviour, chick acceptance, parental behaviour and nest-building before and after the eggs are laid. Uli hopes to get up for a few weeks in the chick season to go on with the pecking response stuff.

Fae wrote us that she had seen you briefly when she passed through the East and that you didn't get round to talking shop until it was much too late to talk seriously about anything. She doesn't seem to be having much fun at La Jolla and can't get her fish nor do the facilities seem good (she says 10 times ^{as} than at Oxford !). But you probably know this already.

David Snow is off in a few days to Trinidad. Still unmarried. A useful acquisition here is John Godfrey, Aubrey's predecessor at Edinburgh, who is now living in a house-boat here and working at Harwell. He comes to Friday evenings and is a bright spark. No more chat now.

Yours

Dike

Comments - Gull & Tern conference, much amplified. Copy to Patri & Frank.

During the recent summer I have had a chance to look at and compare 4 spp. of terns as there were nesting on the Inner Farne Common, Roseate and Sandwich as well as the Arctic. The three other spp have nested in other years ~~too~~ but in less numbers and I haven't had much chance to look at them. There are some interesting differences which I thought you might like to hear about. ~~xxxxxxxxxx~~ As I think I may have told you before the Arctic and Common terns seem to have an almost identical behaviour. I conclude this from my own obs and those of the Dutch fellow, Schenk, who has been looking at the Common tern. The Sandwich however is different from them in a great many ways, both morphological and behavioural:

1. The colonies are far denser and the young are led away from the nest soon after hatching.
2. Presumably adapted to this last difference much behaviour is lacking to conceal the nest which is present in Arctic & Common. The brooding adults do not fly away from the nest to defaecate but do so a few inches from the nest and the young do not walk away to defecate; ~~further~~
3. the egg shells are not carried away when the young hatch. ~~Not are the eggs so cryptic~~
4. The "normal" aggressive response of a ~~bird~~ ^{S.T.} to another is the gekkering. This might of course be because the ~~birds~~ are so close together but I have indications that it is not merely this. ^{The difference seen to be in the} As I think I wrote you once before ~~un~~ I know what the gekkering is homologous ~~with~~ in the Arctic and Common but it is rarely to be seen unless the intruder comes close to a bird who is unwilling to leave its nest to attack, say a brooder. I have not been able to establish any homologues of the Arctic's normal aggressive behaviour in the Sandwich though some elements may perhaps be recognisable. Incidentally in this gekkering the crest is strongly raised, as you know, while this structure is almost absent in Arctic and Common.
5. One of the most conspicuous calls of the ~~species~~, the Fish call (though a fish is not always carried when it is given), seems to play an important part in pair formation and maintaining contact between the two mates and probably also between parent and chick. This call does not occur in fights and there is no reason to think it is aggressively motivated. Arctic and Common seem to have a call which is charcateristically associated with a fish but this call also occurs commonly in fights, and is clearly aggressive.
6. The food begging is somewhat different and more gull-like. In Arctic and Common the neck is withdrawn in food-begging, into the hunch posture. The calls are then uttered from this position, the bill wide open without head tossing or bobbing, and the calls, even at low intensities consisting of "bursts" of individual syllables. In the Sandwich there is the same withdrawal of the neck into the hunch posture but ~~then~~ each call is more single and is associated with a clear head tossing movement. Only at high intensities do the single calls become run together and even ~~then~~ then they are more irregular than in the other two spp.
7. Of the morphological differences you probably know more than I do. The most striking (apart from the crest) are the plumages of downy young and the first juvenile plumage. There are also such features ~~as~~

such as the dark outer web~~s~~ of the outer tail feathers in the adult which may or may not be an important character. As you know that's about all there is ~~in~~ which one can use in the genus Sterna!

I have sav d up the Roseate tern until now so that I may spring on you the fact that judging from behaviour alone he seems to be almost a Sandwich tern. The normal aggressive call is the gekkering (almost indistinguishable from the Sandwich's) and the slight crest (he has rather more of one the the Arctic & Common) is raised as are all the feathers of neck and back just as in the Sandwich. There is clearly a fish call which doesn't seem to be used in fights but which is used to maintain contact between the pair. The food begging ~~consists~~ of individual syllables. With regard to the density of nesting I cannot decide from my own observations as the Roseates have never formed themselves into a colony of their own on the Farnes. On the other hand the Marples say that in Ireland they tend to nest ~~in~~ more densely than Arctic and Common. ~~xxxxxx~~ Unfortunately Vouz, who has looked at colonies of Roseate and Common nesting separately in the Dutch Antilles, says that the Roseates are no denser than the Common. To return to my own observations some aspects of the behaviour etc seem to be "cryptic" while others are "colonial". There seems a tendency to rest in the middle of a tu-sok, quite unlike the other spp - any of them! The young usually (?) leave the nest to defaecate. I don't know about the adults from direct observation but presumably they do also for there is not the ring of droppings round the nest even before the young hatch which is so typical of Sandwich terns. Both eggs and young are much browner than Sandwich terns and to my eye are more cryptic. The colonial-like or non-cryptic features are (1) not carrying away egg shells and (2) leading the young from the nest soon after hatching. My case for arguing that these two characters are non-cryptic is of course not a very strong one and rests entirely on the evidence from the Sandwich tern where these features seem directly concerned with the dense nesting. It is I suppose possible that the lack of egg shell removal might have an entirely different explanation. For example that since the Roseates' nests are so often in tussocks the egg shells are ~~xxx~~ not conspicuous to predators. However the existence of the other behaviour similarities between Roseate and Sandwich suggest - no more - that it may be more closely related to the Sandwich than the Arctic and Common.

I have just thought of two more resemblance between Roseate and Sandwich which I didn't list before. Both seem to lack the maintained tilting of the ~~xxxxxx~~ black cap away from the female which is so typical of Arctic and Common. The Sandwich has in these situations a rhythmic rotary movement of the head which presumably has the same function. I don't see any such movement in the Roseate but I may not have watched enough as the movement seems uncommon in the Sandwich. The other resemblance between Roseate and Sandwich is their lack of predator defence. ~~They are usually extremely alert to predators, and when~~ ^{Predators} in flight ^{they} are very reluctant to attack ~~them~~ in the way which is so familiar in Common and Arctic.

In addition to the behaviour characters the Roseate resembles the Sandwich in some morphological features too. The young have the "spinous" down ^{of the Sandwich} so unlike the Common and Arctic and the juvenile plumage is also like the Sandwich but quite unlike the other two. The outer web of the tail is also like the Sandwich and unlike the others in being white. It may be no coincidence that the grey of the back and wings of the Roseate is the very pale grey of the Sandwich and not the darker shade of the others.

Unfortunately I do not know whether anyone knows much about the systematics of Sterna. Do you happen to know anyone in the States who would be worth consulting? When I came back through Amsterdam I met Voous and was able to ask him about a few of these things but there was no opportunity for a proper talk. He was of the opinion that one could separate off the larger, crested "Thalasseus" type from the typical Sterna but felt that the Roseate should be ~~be~~ separated from ~~either~~. Incidentally he thought that Hydroprogne might well be put in with Thalasseus, a view which had suggested itself before to me from Bergman's paper and which was reinforced twentfold when I saw Bergman's film. The Sandwich tern people at the gull conference ^{for sure} felt that with the exception of one small part of the behaviour, the first phase of the Fischbeugung, the behaviour of their sp. and the Caspian were identical. The only pity was that Bergman himself wasn't able to say what he thought of the Sandwich tern film to see whether the view was mutual.

So much for the comparison of the 4 spp. I could watch. There is another point which might interest you concerning the movement which accompanies the Fish call (the loud "koreet") of the Sandwich. When uttered by a bird on the ground the bird makes a more or less distinct head tossing movement as it makes the call. Apart from the movement itself I do not know that there is any reason to equate the movement with the head tossing of food begging. It may be and often is uttered by a bird carrying a fish. I have seen signs that the head tossing with koreet can grade into normal food begging, for example when a brooding female calls to her mate when he brings a fish for her and eventually begs when ~~she~~ alights at her side. From what I saw on the film and from Bergman's paper the Caspian tern also has a similar movement at the end of its Fischbeugung which resembles the head tossing of a food begging bird. Look at photos 5, 7 and 10 in his paper. The movements seem (to me) to be homologous in these two spp. but I would doubt their relation to food begging, or indeed their origin from food begging were it not for the occurrence of a similar head-tossing-like movement at the end of the Long Call Display in the Laughing Gull and also, as far as I remember, in some of the spp. you have looked at. I recall that Niko violently rejects the idea of the last phase of the Herring Gull's trumpeting as having anything to do with food begging but do you not have so more arguments for this? I would be glad to hear of any new ideas which you might have to explain the occurrence of this movement in this context. Perhaps it might help for the terns.

Goethe Herring and Lesser Black backed.

Ontogeny of the long call. The different phases develop at different times. The last phase, the pointing up one, is the first to develop at an age of a few weeks. The earlier phase(s) appear later, at a couple of months.

Recognises something which he calls the Forward but it is only very brief. It differs from the Hunch in neck being more stretched out and back feathers (?) less erected. Doesn't know about carp. joints. Feathers of forehead not raised.

~~Kittiwake~~ Herring and Lesser black backed gulls differ in that one of them matures earlier than the other. The "Herring" gulls of the Carmargue, which he has reared in captivity, resemble fuscus in this respect and also the calls of the Carmargue birds in nature is very like ~~thick~~ fuscus and unlike argentatus.

Esther. Described the kittiwake's repertoire of displays and discussed the unrewarding task of trying to homologise them with those of the other known gulls. It's not really as bad as that but there are two postures, the kittiwaking and moan-and-bow, which are not at all clear and ~~XXX~~ another, the kek movement and call, which seems quite unrepresented. Furthermore there is a pre-flight intention with the eye almost closed which is problematical. Niko thinks that the kittiwaking is the long call and that the moan-and-bow is the mew call and posture of the Herring gull and feeding call of the blackheaded. This might I suppose be true judging purely from the form but I am suspicious of using form alone in such ~~unrelated~~ spp. If he is correct then the motiv must have changed very considerably, for the kittiwake's moan and bow is the most aggressive posture there is and is never used against the mate. I am prepared to be convinced but am not convinced yet.

The relation between the kittiwake's jabbing (I think you know what we mean by that) and the forward of the BH gull was a point which she didn't have time to discuss though I think it might have been valuable. What is the relation between these postures and the hunch? In the kittiwake it seems to be more or less accident that the posture from which one bird jabs at a neighbour looks rather like the hunch. For that matter it looks like the resting posture too. The jabbing seems to be an intention attack or indeed an actual attack delivered by a species which for various reasons related to cliff-nesting doesn't try and peck down on its opponent. In your thesis you write that you believe the Forward may have something to do with the Hunch. I wonder how far you still believe it now.

Incidentally this might be a good place to mention an idea that has been dawning on us this season concerning the food-begging.

The food begging of the young ^{and adult} Arctic terns is usually in the hunch posture but if they are very eager to get the fish they may adopt wh at I call the Erect Food begging posture with the neck stretched upwards but otherwise like the Hunched food begging. A bird ~~ad~~ may adopt the erect food begging on first seeing its parent or mate but as the two come closer together the ~~xxx~~ neck becomes mor e and more withdrawn until the hunched posture is assu med. The erect part of the food begging seems to be designed to make the begging birds as conspicuous as possible, which it would often not be in the hunch posture where there was vegetation. From the observations we made on ~~a~~ herring gulls

and a black headed which we reared from hatching, ~~km~~ we got the impression that there was the same sort of effect in the erect and hunch phases in the begging of these chicks, except that instead of a ~~small~~ shift from the erect phase to the hunch, ~~xxxxxx~~ the two phases alternate but the hunch becomes more and more predominant the closer the chick gets to its "parent". Certainly we got the impression, and I think that Uli and Rita agree, the top phase often ~~m~~ makes the chick conspicuous in places where it would be hidden from view if it ~~xxxxxx~~ be ged only in the hunch. What they don't altogether agree with yet, though they haven't specially looked, is that the top phase becomes less and less ^{present} the closer the parent comes to the chick. If we are right on this point it would seem probable that the erect phase of the tern's food begging is homologous with the erect phase of the gulls'. I have carefully avoided bringing the adult gulls into the argument because I understand that their food begging is rather different from that of the chicks. However it might perhaps be possible to incorporate this too. You write somewhere in your thesis I think that the bottom phase of the female's begging ~~xxxxxx~~ i.e. the bottom of the "bob", is identical with the hunch. Where does the top of the bob come from. Is it merely an alert posture or even a resting posture? Or could a part of it have been developed specially to make the female conspicuous. From what I recall of the black headed film the female plagues the male enough by her presence without having to make herself more conspicuous than she is. It may also be significant that the female isn't having to compete with other females to get the male's food as are the young gulls and for that matter both young and adult female terns.

This interpretation of the ^{function of the} top phase of food begging is supported by the kittiwake since in this species food begging is in the hunch and there is no long neck phase. Almost all feeding takes place on the nest in this sp so that there is no need for the female or chick to make itself conspicuous.

In the absence of Bergman, Goethe and Esther's talks were the only ones about gulls. Baerends had decided there was no point in discussing ~~nest~~ building wh ich his people have been working on in view of the fact that Uli and Zahavi, who had been working on it at Ravenglass this summer were neither able to stay for the gull conference. And in any case the nest building is not really part of the comparative studies which the conference concentrated on in the brief two days it lasted.

Schenk talked about the aerial display of the Common Tern. His account agrees very much with mine with two exceptions. My account you have read already in that report for the Natural History Society people who administer the Farnes. The difference in our two stories may well be related to the fact that his main observations were made before the birds alighted at the colony at the beginning of the breeding season while mine were made after this time. His facts may therefore represent an earlier stage than mine in the ^{second} cycle as a whole though not, I believe, in the sequence of an individual pair formation. I described as different displays what I called the Fish flight and what I called the Advertisement flight. According to Schenk the Advt flight is the beginning of the H. flight and they are not separated, as I thought typically, by the birds landing together on the ground. The other difference between our two accounts is that he thinks that either male or female may be the pursuer in the high flight ascent, and that there is no change over in the roles at the beginning of the glide of the high flight.

With regard to the motivation of the displays we are no farther forward than before. Certain parts look rather aggressive but never, or hardly ever go into attack. If a third bird joins in the display and overt aggression raises its ugly head the whole form of the display alters. Lastly, aerial fights between birds hardly ever go over into genuine aerial display. In spite of all these difficulties I believe there might once upon a time have been an aggressive origin to this behaviour and the gulls' aerial ~~xxxx~~ ceremonials makes it look all the more likely.

Concerning the function of the behaviour Schenk and I are more or less in agreement that it seems to test the bond between the pair.

van den Assem was unfortunately unable to be present as he is doing his military service. However there was present a girl called Angela Bol who had ~~xxxx~~ made a study of head shaking in the Sandwich terns and was very familiar with the spp., and also a man called Groot who had made the film of the Sandwich terns which was shown and himself knew something about this species.

Bol gave a talk about the S. tern and the following information comes from her speech together with replies to questions I asked her at the time and after seeing the film. Some of the things I have mentioned before in connection with my own observation on this spp in comparison with the Arctic, Common and Roseate on the Farnes.

The gekkering you know. It seems often be followed by fixation of the ground in front of the bird in a way which shows off the crest. No origin to this fixating movement is suggested. I have seen in the Arctic tern what seems to be a very similar thing in ~~xxxx~~ similar situations. namely after threatening, but I too have no suggested origin. It may perhaps be that this downward movement is incorporated into the bowing or nodding display of the Arctic tern which you have seen yourself in hostile situations.

I may mention here that Caspian tern also has a similar pointing down movement, Beggman's aggressive intention bow, but I do not know for certain if I ever saw the movement on the film. As he describes it there it does not seem ~~to be same~~ the fixating of the ground which follows gekkering in the Sandwich tern.

There is nothing which the Sandwich tern shows on the ground which is clearly the Beugestellung of the Common and Arctic (although there is an aerial Beugestellung). There is however a posture whose homologue is unknown in Common and Arctic in which the neck is stretched up and the bill pointed more or less vertically downwards. The two mates (but apparently not rivals) approach one another in this way and almost push their foreheads together, each

of them adopting this posture. The behaviour is often followed by scraping. Nothing is known of the motivn or function of this posture. (See below for reason identifying this posture as S.Tern Beugestellung)

The Reckstellung seems to be the one redeeming display which all the terns have though in the black tern and Caspian it seems sometimes to be accompanied by a call. In this position ^{almost} all species seem to make some kind of movement: Arctic and Common tilt their heads on one side, Sandwich and Caspian rotate the head to and fro, while the Black tern turns its head from side to side in what seems to be a ^{rather} similar way. Only in the Little tern has no movement been noticed.

The S/Tern's aerial display was described by Bol. It is less ritualised than in Arctic and Common (I have seen it myself and can corroborate this). Apparently the fish may be exchanged one or more times in the air! I haven't seen this myself. Although the display is less ritualised I gathered there was no indication that ~~xxxxxx~~ its motivation was clearer.

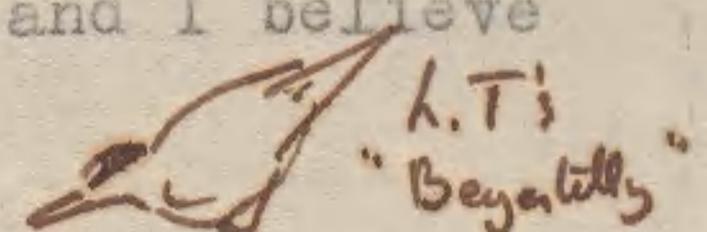
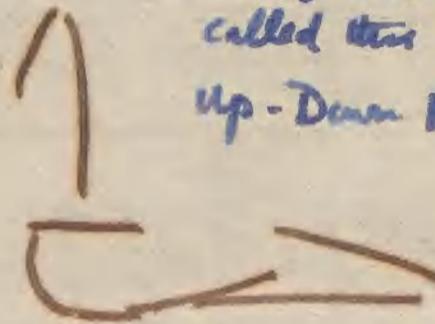
Roeth told something about the Little Tern but I don't think he said very much more than three years ago, though I do not at the moment have my notes by me from then. His talk was rather side tracked by a long discussion about whether he was justified in concluding that the erection of the tail was a measure of aggressiveness.

The little tern seems to have a very peculiar feature completely lacking in the other spp. This is a curious swinging of the head from side to side by the male in pre-cop. This is as about as odd as the kittiwake's kek display. ~~No connection with other spp. & may be suggested.~~

In the aerial display both bent and stretch roles occur and on the ground the stretch is clearly like the other terns. However the bent, the Beugestellung, is much more bunched up than the Common and Arctic and instead looks more like the analogous (and I believe homologous) display of the Black tern when the mates come together. This has been called Stooping in the black tern. ~~Roeth~~

In "pure attack" the little tern points his bill well below the horizontal and runs at the intruder without any call, but with the tail raised. Is this pointing down of the bill the same as I mentioned in connection with the downward fixation of the Sandwich and the bowing of the Arctic?

[In my thesis I have called this the Up-Down Posture]



Baggerman. Finally Bep Baggerman spoke about the Black Tern but again she added little to what was said last time. The stooping posture, the analogue of the Beugestellung, looks rather like what is an intention to scrape in the Arctic. The black tern never scrapes but in two situations where the Arctic scrapes the black tern adopts a posture which is not distinguishable from stooping. These situations are immediately following the arrival of a female, as part of the greeting and in order to attract the young. Possibly the Beugestellung of the Black tern is derived from scraping, which would imply that it must be also in the other ~~spp.~~ spp. too. There is certainly some kind of close connection between these activities in the Arctic but there are differences too which are difficult to explain. This possibility would throw light on the unidentified display of the Sandwich tern of which I have made a picture in which the birds stand head to head. For the one thing which is certain about this posture, as far as I was able to discover, was that it was often followed by scraping. Why an intention movement of scraping should look like that in the Sandwich tern is of course still unexplained. There remains one important point which is unexplained about this posture and that is why it should occur in such a widespread way in the aerial display. (NB: I still think there is no doubt that the aerial Beugestellung is the same as the ground one.)

These accounts of the talks are, as you will understand, liberally larded with my interpretations of the observations and are not necessarily the opinions of the speakers. But to give you an idea both of what was said and of how it seemed possible to interpret these things I thought to set it out like this. Some of my ~~xxx~~ details may be rather tedious for you but I don't know how much you remember of and are interested in the terns. Considering that there were ~~7~~ spp. of terns discussed at the conference I get the idea that there is less similarity in their behaviour than in a sample of 6 gull spp., such as those you describe in your thesis. But it may be just that we ~~don't~~ don't know our birds as well as you knew yours. And of course it makes all the difference to have seen something of all the spp yourself.

• January

Zoo Dept.,

Oxford.

Dear Martin,

Many thanks for sending us your summary on Aerial Hostile Patterns. There are a few points we would like to ask about. In your letter you say that all the calls (of certain spp.) seem to develop from the distress call of the late embryo and newly hatched chick. Why distress? Is this different from the food begging call?

The mention of Rissa on p.4 is presumably a misprint for ~~xxxxx~~ Sterna.

Esther says that what you tell of the Plaintive Charge Call reminds her of the "wake" of the "kittiwake" or of the moan. Whether these two ~~things~~ calls have a common origin she seems unable to say. It would be nice and simple to think so but apparently in the aggressive kittiwaking when a bird is really excited the second syllable ~~sounds~~ ^{becomes more emphasized but} much less like the moan than it usually does.

The business about special postures shown by the flying juvs. sounds most interesting and important. I have kept a look out for this in the young terns after I saw in 1953 that a young Roseate ~~etc~~ did the stretch a number of times when its parent landed near it. I am satisfied that the young Arctics rarely do a stretch ~~but~~ ^{probably} some individuals more than others. It occurs in much the same situations so far as I could judge as the adults would use it. I could never distinguish any other "courtship" posture by the young, except of course the hunch which in any case is difficult in the terns to distinguish from the resting posture. You will doubtless tell us in your summary at what age you say these new postures in the flying juvs. It may well be that since I only watch my young terns for the few weeks after they can fly before they leave the island ~~they will not be seen~~ I would not see them if they occurred.

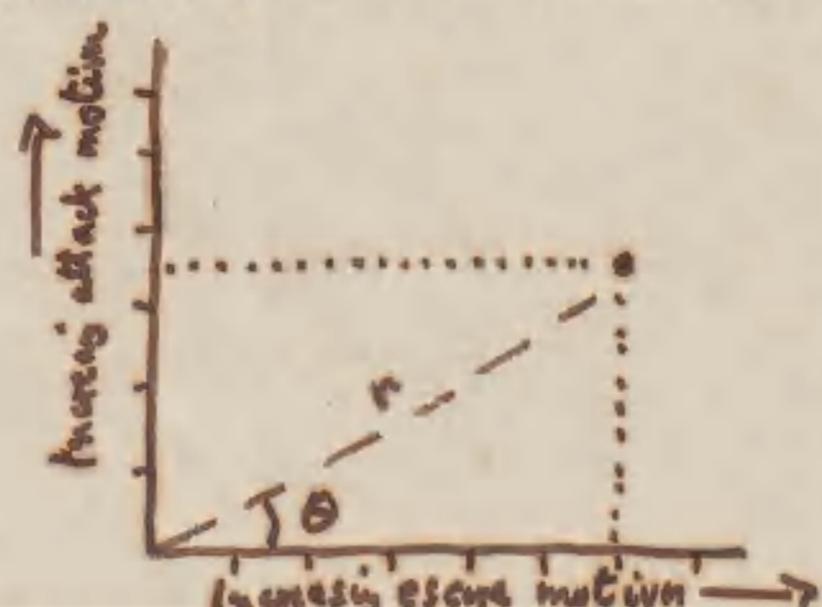
I am not convinced from your description about the difference between the Swoop and Soar and the Swoop, Rise and Hover, that is if you mean by using capitals, and I believe you do, that these two things are somehow differently ritualised. It would seem at first that they are merely different responses depending on whether the object threatened is more or less mobile. Or perhaps, from what you say on p.6, you think the same. No, from your motivation diagram it is clear that you think the level of drives is different in the Soar and the Rise.

I have tried to set out a list of calls of the Arctic tern followed by a review of the calls of several other spp. I tried on a set of basis for homology in the different spp.

You list a number of calls of Franklin's gull. I wonder if you have worked out the homologies between the calls of the various gulls, and in particular how you have managed to fit in the kittiwake. Food begging, choking and the (rare) alarm call are clear enough but the kittiwake call, the moan and the "go" call seem difficult at the moment but perhaps with your wider experience of the Larids you can include these too. For example we don't really see why one should call the kittiwake the long call as Niko does in every public pronouncement on gulls. But perhaps you can distil from the several species you have looked at some common characteristic of the long call and the other calls which would enable homologies to be established. One of the main catches about the kittiwake call as being the long call is the idea that the kittiwake call may itself be ~~more than~~ a combination of the choking call and the moan. The combination has certainly be ritualised, whatever that means, but is not completely implausible though difficult to prove it seems. Your mention of the plaintive charge call of Franklin's gull makes one think of the mew call of the herring gull and the moan of the kittiwake. What about the black-headed?

I wonder if you have tried establishing homologies between gulls and terns. I see you relate the attack call and the gakkering, or what I call the chatter. Don't the gulls have a growly call at nest relief typical of the broody bird? I don't know where I have this idea but if so it would seem to be like the soft call which I think is found in the terns. But perhaps you have set out some of these things in one of your later summaries.

I am filled with admiration for your motivation diagram explaining the aerial display. I wonder how you arrived at it. We find that as soon as we start, complications and contradictions set in very quickly. Incidentally we found it easier to represent the motivations on a two dimensional diagram than with what Esther calls factory chimneys. The main advantage seems to be that one can then more easily express the variation in motivations which gives rise to a posture. Thus any pair of factory chimneys can be represented by a point, just like the coordinates of a graph. But if you want to express that the same posture can occur, for example at variable amounts of attack drive while the escape drive is constant, then instead of having to make two or three pairs of chimneys, this is represented by a line on the diagram. Or if both attack and escape can vary over a certain range independently and yet the posture still occurs, this is expressed in the diagram by an area. There seems to be another advantage of the method. The polar coordinates of a point (see diagram) express the two things which you observe in your counts of what precedes attack, etc. The likelihood of a posture leading to attack is shown by the angle θ while the "intensity" is shown by r .



I enclose such a two-dimensional diagram based on the differences in motivation which you sent me for ~~xxx~~ Franklin's gull. It may well be that you have already evolved this method yourself. I think it is the logical outcome of your factory chimney representation. In fact both Desmond and I arrived at it independently while I was on the Farnes and he was in Oxford. But I think that his method is slightly less generalised than it should be. There seems no advantage in restricting as he does the space over which the motivations produce a posture. In any case this is a mere detail. The essence of the method is the representing a pair of factory chimneys by a point on the graph.

~~in Estor~~

Have you been driven to the conclusion that ~~she~~ has in the kittiwake that the particular quantities of attack and escape motivation which give rise to a particular posture are different in male and female? I suppose one must conclude this when you see that the greeting is very similar if not identical in its main form but that the male is far more likely to attack the female, and she to flee, than vice versa. Presumably it is something like this which makes the male black-headed gull head flag first ?? It can hardly be that he is more frightened of the female than she of him. Or could the sex drive rear its ugly head at this point?

No more for now. Shall write again when we hear more about your work from the summaries. Many thanks again for the first one.

You
Mike

The table showing the frequency of postures in different situation has been arrived at without counts. I have not been too successful in attempts to count these things - we have tried it mainly in the Kittiwake - and I wonder in any case whether one would get much out of using other people's counts ~~or anachronisms~~. Certain points are obvious about differences in intensity of postures and these one can describex in words and I think that counts made by different people would only give one a false sense of certainty. Perhaps I am too defeatist about these matters as I have not seen how you make use of your counts in comparing the motivation in different species. One of the points which worries me is that, so far as I understand the method, it assumes that a dispute, say on the communal area, ~~xxxxxx~~ produces roughly the same kind of motivational situation ~~as~~ in one species as in another. And I am not too certain that this is true for some of the species I have been looking at - for instance Sandwich compared with Arctic Terns. In these two species the difference in nesting density seems to me perhaps to alter the motivation produced in the stock situations. Likewise in the Kittiwake is it not possible that the proximity of nests on the cliffs means that comparisons of territorial encounters in this species with the B-headed G cannot be made very closely. In other species where ecological conditions are more constant, I dare say that these objections are quite groundless and one can make the comparisons without such drawbacks but I hope I make my clear the reasons for my doubts. I look forward very much to seeing how you use your counts in comparing species. Was it incidentally by means of the, that you produced those wonderful ~~xx~~ phallic diagrams looking like a longitudinal section of an onion, describing the motivation of postures in the B-h and Franklins Gulls ? We never heard how you accounted for some of the intricacies of these figures. Whenever we have tried, we have quickly ended in some self-contradiction suggesting that there are more than two parameters involved. How many "simplifying assumptions" did you need to make ? I am not trying to be funny but we are genuinely interested to know how you have extricated yourself from the sort of motivational impasse which we found ourselves led into.

Niko is due back in a week and then I shall perhaps see your new reports about the Inca Tern et al. I wonder very much how they fit in with the ideas which I have come to. ~~xxxxxxxxxxxxxxxxxxxxxx;~~
~~xxxxxxxxxxxxxxxxxxxxxx;~~
~~xxxxxxxxxxxxxxxxxxxxxx;~~
I am still stuck to find this in the Arctic though there are two ~~xxxxxx~~ possibilities. The trouble seems to be that the terns - at least those species I have looked at - don't attack by pecking downwards and one would not expect to find an aggressive upright (unless it is a relict from an ancestor). All the species I know attack by a horizontal peck so far as I can see. Any ideas ?

* the Aspirine Upright

December
16 November

Zoo Dept.

Dear Martin,

This letter breaks a very long silence, but we have been rather busy with a report since we got back, which was designed for the natural history society who allows us to use the quarters on the Farne. Niko said that you would like to see some sort of account of our work in the last couple of years so I am sending you the reports such as they are. They are very unsuitable for your eye as we appreciate only too well. We have glossed over many difficulties and left unsaid many things which you will be curious about. All the same ~~unimportant~~ some points may be interesting. There is a good deal of padding in my reports, especially on the non-reproductive sides because I wanted to give the impression that we were occasionally interested in other things than how the little creatures procreate. But you and I know that nothing else could be so absorbing ?? We hope to go back for one more season though only a short one as I must start writing up this winter and I would like to get the shag stuff finished. At any rate we don't plan to go back much before the terns arrive and as they are supposed to be my thesis subject I ought to be more interested in them than the shags, which I certainly am not. However I plan to return to the shags in my old age. The terns are rather difficult from many points of view as I hope I make abundantly clear in my report. The first difficulty is to try and discover how the pair forms let alone anything about motivation. That has occupied me most of the time and I had almost given up hope until the light suddenly came to me at the end of 1954 which fitted several things together but which I had succeeded in closing my eyes to for the best part of two seasons. But that's only the beginning and I can't see that I am likely to progress far on the motivation, for example, of the aerial display. However my views ~~at~~ the motivation of various postures are as they stand in the report though there I haven't been able to explain my reasons fully. I shouldn't believe anything I say too much as my conclusions about motivation seem to rest on so many preliminary assumptions which, from what I have seen in the shag, are capable of being reversed after next season's watching. This isn't just one's natural pessimism but a more serious cause of dissatisfaction. I find that I see so easily just what I want to see

that I mistrust the most harmless observations.

On the ~~xxxx~~ behaviour other than courtship and threat display I am more sure of myself but I think that interests you less. The threat and courtship seem to have gone quite a way on the road of ritualisation and although its simple enough to talk about recognising elements of attack and escape this doesn't seem to explain very much. At last I have got even Niko to agree that the tern's aren't as easy as he thought they might be but he always says "but think how much more you know about the tern's behaviour than anyone else". It's scant consolation when one compares it with your scheme in the BH gull or even Esther's ideas about the kittiwake. It is very striking to me how much easier it is to understand much of the shag's behaviour than the terns, because the shags move so slowly and their changes of mood are correspondingly slow.

Niko thought it would be a good idea for Esther to publish a short paper based on the report for the Ibis or something and that is occupying her time at the moment. She would like it to be a bit more accurate in details than the report!

We've been very glad of the chance to see the two papers you sent to Fae in order to see which way your thoughts are turning since you left Oxford. I think that Fae has handed on to you some of my comments. Most of the things were more or less trivial but there were some more important objections. One of the ones I feel most heated about is your discarding of displacement grass-pulling. If you had ever seen it you would see at once that the movement of depositing the material is the nest building movement. And in any case when a gull has something in its beak which it wants to get rid of it shakes it off in a quite different way from what happens in grass pulling during fights. Incidentally Esther was reading Steinhäuser (1938) the other day and saw that he said that the gull treated the grass just as it would like to grab the opponent if it dared, so he clearly recognised the redirection element. I am sure you can't completely throw out all the displacement element in grass-pulling but I think that there is a quite "simple" explanation of why the redirection grass pulling should be followed by sideways-building - namely that the movement is stimulated by the presence of ~~xxxx~~ nest material in the beak. If there were any likelihood of some displacement activity occurring ~~xxxxxxxx~~ this would explain why it should be this particular one. Exactly the same argument would account for the observation ~~xxxx~~ that when you crowd male sticklebacks the head-down threat goes into sand-digging, though here it is presumably the influence of the posture which determines the displacement activity. I was very impressed by the link between certain activities (in no sense in displacement situations) apparently as a result of the similarity in the posture. In these cases I think I could conclude that the influence from the posture was a proprioceptive one. Of course ~~xx~~ some of the examples of "influence of the environment" such as the stickleback example may be partly

proprioceptive. The two best examples I have of this are mentioned in the report. The business about deriving the cormorant's "wing flapping" display from the both-wings-stretch hasn't much to recommend it except ingenuity. I don't think I believe it myself.

On the matter of displacement activities I have found several examples of their occurrence in "low intensity" situations. I remember you once asked Fae about something I had suggested about their occurrence in these circumstances as if it were not to be expected. I don't think there is much reason to believe there is any general rule about d.activities appearing only when the motivation is strong. The hostile nest quivering in the shag is the activity I have paid most attention to with this in mind and there I have no doubt that it expresses a lower intensity than the shake gaping which comes near to being intention movementx. Preening of the mate also occurs when a bird is insufficiently motivated to mount but not because there is any strong conflict.

By the way you say somewhere in your thesis that the thick neck of the b-h gull is due to tension in the epaxial and hypaxial muscles. I wonder do you still think so and why. We have examined the neck anatomy of several gull and it seems most unlikely that tension in the neck muscles is ~~xxxxxx~~ could produce any appreciable swelling of the neck. But we don't know if you conclude this from dissection or not. On the other hand erection of the neck feathers certainly could produce such an effect and from Esther's observations in the kittiwake is almost certainly responsible in that species. This is supported by the position of the groove in the neck in such a thick-necked bird which seems to correspond with the apteria on the sides of the neck. This seems to work in the kittiwake and herring gull where there are photos which show the position of the groove rather well but I don't know yet about the b-h gull.

In the choking of the b-h gull you concluded that there were several elements which were not derived from nest building including raising of the ventral feathers, depressing of the tongue bone, and opening and shutting of the cloaca. Are the "ventral feathers" the same ones as those erected when preparing to brood? From your own picture it looks rather as if this is not so. In any case in the kittiwake and herring gull a close examination suggests that the main feathers which seem to be raised are the lateral flank feathers and that they are passively moved by the shift in relative position of the bird's body and legs as it tilts forwards. About the hyoid Esther thinks that this may(almost ?)always be depressed when the bird utters a call. Certainly it seems to be in most of the photos of the herring gull in Niko's book. Of course when the bill is opened the effect won't be so strong but Plates 2a and 9 seem rather convincing, for example. Finally do you know that the gull's cloaca doesn't open and close when any call is uttered

intensively. As you will have guessed there is a reason for her objections. She wants to derive choking from the movement of depositing nest material in a relatively pure state without the complications of superimposed broodiness or ~~sex~~ sex or what have you. At any rate she can talk herself into believing this in the kittiwake and wonders how far it may be true in the other species too. Incidentally we have seen this movement of depositing nest material in the herring gull where its form is much as in the kittiwake but instead of being repeated a number of times, only a few jerks are made at the most. This seems partly to be due to the kittiwake's nest material being more sticky and partly to some intrinsic (dare I say innate) difference.

You will have heard that head flagging has been seen now in the herring and lesser black backed gulls. I don't know if Fae told you that the herring gulls have a well developed greeting ceremony: mew call, choking, head flagging. Back to the herring gull indeed ! We don't have time to watch it properly but ~~the~~ black headed gull work has put us onto lots of things which are at once obvious.

Does the b-h gull tend to go to its nest or a potential nest site to choke ? It looks very much like it in this greeting-choking in the herring gull and Esther thought that this might be a sort of reason ~~why~~ the kittiwake, who of course stays on his nest site all the time when he is on his territory, should use choking for the song.

Well this should raise enough bones of contention - to mix a metaphor - to get us along for a time. I'm sorry we can't talk it over as we should probably get ~~across~~ your ideas more exactly, and I dare say there are many provocative things in Esther's report you would like to know more about. When you can find time to write we'll see what we can do to satisfy your doubts and curiosity.

Yours

Mike.

Zoo Dept.,

20 December 55

Oxford.

Dear Martin,

Thanks for your letter. It was most tantalising to hear about Larosterna; I am only sorry that you didn't describe any of its postures. I hope you will be able to let me know something about the form of the movements at some not too distant date. It must be an astonishing creature, and it made a great impression on me from the first time I saw it in Murphy.

In answer to your questions I think you will find that some points have been answered in the report on the Gull & Tern conference which I sent to you via Frank some time ago. If this hasn't yet got to you let me know and I will stir up Frank, though as you probably know he is having great worries at the moment as Brenda has severe cancer.

The Dutch tern people don't seem so interested in the comparative approach to the terns and concentrate more on counting postures and things like that. However the comparative side interests me quite a lot, though from the point of view of radiation rather than taxonomy - if you see what I mean. I come more and more to the view that it is extremely difficult to compare on the strength of the observations of other people especially if those people haven't seen more than one species. Consequently I am happiest in comparing the four species which I have seen: Arctic, Common, Roseate and Sandwich. Bergman's film eked out by his paper (and vice versa) are also useful because the Caspian is so similar in many ways to the Sandwich. On the other hand the Black Tern is sufficiently different from any of the other species for me to find a comparison of the calls, for example, extremely difficult even after having seen a little of the beast. I dare say if I saw it after having watched the other species I should understand it better than I did when I was just beginning to know my own species.

All this comes as a preface to an attempt to tell you something about the calls of the Arctic and other species of terns. What I shall do is this. First I will tell you about the Arctic's calls and then give a table purporting to set out the homologues of the different calls so far as they are clear (and in some cases perhaps where they are not). At the end of the table I have tried to give an idea of the character of the call common to its forms in all the species, which should assist in determining the homologues in other species.

the Chatter.

6. The next call, ~~ky~~ is given by birds who swoop down to attack a predator in the colony. It is the familiar "tikitikitik..." This call is also uttered on the ground e.g. by brooding birds when others approach near, or when a rabbit or some other species comes close to the brooder. On the ground the bird stretches towards the intruder as far as it can without rising. I haven't been able to detect any feather erection. I have little doubt that this has a common origin with the gekkering of Roseate, Sandwich and Caspian.
7. At the bottom of the swoop at a predator the Arctic tern calls a loud "kyow", or something like that. This seems to be a different call from the chatter and can be heard on other occasions too. When two terns are fighting in the air and ascend in an upward flutter the same call can often be ~~kyow~~. And it may be heard, with or without the chatter, as a tern attacks another. The call seems to come at the moment of closest contact with an opponent.
8. It is sometimes possible to change the "kyow" last mentioned into another call. If a tern is swooping at you with the "tikitik" and at the last moment you jump upwards at him, he doesn't call "kyow" but instead a musical "kliu". This kliu is also heard under natural conditions in circumstance suggesting it is rather less aggressive and more frightened than that "kyow". There are two other conditions when it is particularly common: during the ascent of the High Flight, by the following or pursuing bird, and as a response by brooders to a gull approaching the colony when the birds who call leave their nests and attack the gull with the "tikitik kyow" form of attack. The form of the musical kliu does not seem to resemble the loud "kyow" but I think they are rather similar and hope one day to make a spectrographic analysis. In adults
9. Food begging call. A shrill "kee-kee-kee...." at a frequency of about 6 per second. In chicks the call has about the same maximum frequency but each syllable sounds more like "shi".
10. Male copulation call. Before mounting it seems like a muffled ky2 and after mounting and during copulation a muffled ky3.
11. When the adults are handled for ringing the birds occasionally uttered a very shrill, high-pitched "keer". This call is distinguishable from any of the others though perhaps grades into the "keyair". I have also heard it from birds who were involved in fights and were trying to pull themselves away from the grip of another. When they young are handled they give a loud "shri" but this doesn't sound like the "keer" at all. Perhaps it develops into it; perhaps it doesn't. In the chicks this shri seems to grade into the syllable of which the food begging is composed.

Here then, for what it is worth, is my list of the calls of the Arctic tern. The Common tern appears to have an almost identical repertoire though the whole tone is rather different. The most different calls from the Arctic's are the alarm call when you walk in the colony, which is "keyairrrrrr" with the accent on the second syllable which is more drawn out than in the Arctic, and in the calls ky2 and ky3 which

might be written as "keera-keera..." and "korr-korr-..." respectively. Oh yes, and the food begging call sounds very different though it has the same frequency. ~~Kxkxkxkxkx~~ Each syllable sounds more like "kye" rather than "kee".

The Roseate's calls are in some cases very similar, "chik" instead of "jik", and "keeo" instead of "kliu", but there is the addition of the Fish call ("chorik"). This call is not uttered in hostile situations, at least I have never seen it in a fight. In this respect it seems to resemble what I suppose to be the homologous calls of Sandwich and Caspian. The fish call in all these species seems to be uttered typically by a bird carrying a fish, perhaps especially (though not exclusively) by one who is unmated. It is very striking to ~~watch~~ a Sandwich or Roseate hunting and see how when he suddenly catches a fish this call is switched on, and stops when he surrenders the fish. This call is also used in the aerial display ~~Kxkxkxkx~~ (the High Flight) by both partners but especially, I believe, by the bent-role one. The call is used when bringing fish to the mate on the nest and also to the young, indeed when the young moves away from the nest it seems clearly to be by means of this call that the parent establishes the whereabouts of the young. In the Sandwich tern, and perhaps in the Roseate as well though I am less sure, the two birds who want to establish contact with one another, whether mates or parent and chick, call alternately in a very regular rhythm, a method which would seem to assist localisation of another bird amid the hubub of a dense colony such as the Sandwiches form. So much for the situations when the fish call happens. As for the motivation I am at a loss and the other tern people haven't any suggestions. They all seem agreed (and I too) that the fish call doesn't come in fights. By the way it is a ~~Kxkx~~ Sandwich giving the fish call which you have depicted in your thesis, and which you believed to be the homologue of the aggressive upright. There are two birds in the picture from which you took your drawing, the other one is actually calling with the head-tossing movement I mentioned in my report on the gull and tern conference. I don't believe there is any hostility between these two. In my opinion the usefulness of talking about homologies or common origins ceases when one is considering postures such as this which have such a low degree of improbability. I would agree that this posture in the Sandwich might be homologous, in the sense that both it and the ~~xxxxxx~~ upright are ritualised forms of a stretching upward of the neck and a lifting out of the wings. But I have no reason to think that the S.Tern's stretching upward of the neck is derived from an intention movement of attacking. In fact this sp. doesn't seem to attack from above at all but rather from a gekkering position. The stretching upward of the neck seems to me to be more likely a general alertness in the S.Tern. It is for this reason that I don't like to use pure form in homologising movements unless the movements are so improbable that they couldn't have arisen by chance convergence. It is in fact this reason that makes me search for homologues only among closely related species and only when the situations

are similar. This seems to be to be a severe limitation in trying to recognise the homologues of various movements, perhaps more severe than in comparing morphological characteristics. But ~~K~~ all this argumentation rings a bell with me and I feel sure I have opened my heart to you on these matters before. Could you perhaps let me know what you think about all this? Have you in fact encountered these difficulties in your studies or are the gulls sufficiently similar? There is again the difficulty with the Kittiwake which, to judge from the few species of gulls with which we are here familiar is very different from either the Herring Gull or the Black-headed - much more so in our opinion than these two species are from each other, though I note with interest that you put Rissa into the "hooded gull sub-group" rather than the "large gull one". The Kittiwake seems sufficiently different in the form of its movements for us to have great reluctance to say what the Long Call is in this species. Niko says always it is the kittiwake-call but admits there is really no better reason for picking on this than there is to say that the Moan is the long call. ~~Wx~~ In comparing a greater range of gull species you must have found some useful criteria in deciding what the long call is, can you disgorge this information?

By the way before leaving the matter of systematics I note that you feel sabini is more difficult to place than many of the other species. Is this on morphological grounds or behaviour? We have seen a fragment of display of this species on a film of Peterson called Birds of America which has been shown here by James Fisher. There may well be more on the Sabine's gull in the original, I don't know. Anyway from what we saw the bird seemed very like our memory of a black-headed. ~~X~~ Have you seen the film? Or the bird?

When you get my report on the gull and tern conference you will see that Voous had already suggested to me some of the points about the systematics of terns which you mention, namely the inclusion of Hydroprogne with the other crested terns and the intermediate position of the Roseate between the Thalasseus terns and the typical Sterna. What sort of evidence does one use in classifying the terns? There seems so little morphological difference between the adults - at any rate of the typical Sterna. How do you reconcile Murphy (1938) on the pan-Antarctic terns with the evidence of Clay (1949?) and Kullenberg? How do you decide what is convergence and what is genuine relationship?

But I have drifted far from my intended path. I was giving some idea of the similarities of the calls of other species to those of the Arctic. The Roseate has what I have called the Harsh Call, which is utterly un-transcribable. It is a sort of hawk, as if the bird were about to spit. ~~xxxx~~ ~~quite~~ From pure form alone I couldn't place it but it comes in the same situations as the ~~Keeyair~~ of the Arctic and I have once seen wing-raising which is so typical of this call in the Arctic but which doesn't occur ^{with} any other call. In the Sandwich there is no doubt of the similarity of the "waaaa"

and the Arctic's "keeyair". Same situation, same form.

As I have told you in the conference report the food-begging of the terns ~~has~~ ^{has} a different form in the different species. Common and Arctic ~~maxx~~^{maxx} repeat the single syllable in a series while Roseate and Sandwich and Caspian utter single syllables at a time in a more gull-like manner. Incidentally this seems to be correlated with the amount of black on the face of the downy chicks. In the Arctic chicks where the bill is held open for several seconds at a time the black down frames the pink mouth. In the other species where the food begging calls are single there is less black. The black tern also ~~maxx~~ ^{maxx} a series of food begging calls like the Arctic and Common. In my table I have linked together all food begging calls as homologous. Here my reasons are rather from the situation than from the form of the ~~maxx~~^{maxx} calls which show considerable variation not only in the amount of reduplication but even in the form of each syllable.

Some of the homologues in the Sandwich are not sure and in the Caspian even less so. I may have been rather Procrustean (to use your famous epithet) in building up my table but it may be some help to you.

Note by the way that I have havered as to whether the ky2 call of the Arctic and Common should be considered as homologous with the Fish call of the other species or not. Because of the elaboration of this call the form is very different in the different species and because ~~of~~ the situation of this call is wider in the A and C. ^Tthan in the others I have not liked to use the other argument for equating it with the Fish call.

I am not sure whether the information I have given so far will satisfy your questions, so I will give you another list of the calls and displays provoked by intruders, ~~etc.~~

Away from colony Arctic terns may fly around and call keeyair as they do to a human in colony, though less firecely. The same thing seems to happen in the Caspian tern (Bergman p.9). In colony Human intruder provokes mainly "keeyair" as they birds hang overhead, also "jik". Also towards hatching time especially the "tikitik-kyow" swooping attack.

Gulls flying near colony provoke "kliu" calling, flying up and "tikitik-kyow" attack. Pigeons, which are much more feared than any other "predator" I have seen, evoke Panics accompanied sometimes by jik calls, but for the main part silent. However some braver souls may dare to attack pigeons with "tikitik-kyow" and these call frequent "jik" as they fly or perch nearby between attacks. Less powerful opponents, such as rabbits, often provoke "tikitik-kyow" attacks. Other terns may also, but usually they get the aggressive call ky2 if the bird is likely to attack, or the jik or keeyair if it isn't. Attacks may of course be perfectly silent.

An unmated male on his territory gives alarm or aggressive calls to intruders but he also may react with calls which seem to be typical for pairing behaviour, i.e. non-aggressive. As I have written you previously the unmated male silent in his territory reacts to a flying bird by calling the ky2 at it from a posture difficult to characterise which I have called the Slant. This is indistinguishable from a hostile reaction but from the slant he frequently adopts the bent posture with the ky3 call, the growly Soft Call. ^{This is not ~~and~~ a ~~hostile~~ hostile} Some males in fact who seem to be in a receptive mood for females start by a version of the bent and soft call to all intruders, even to other males. If a female lands (which she does silently; there is no landing call) the male may parade in the bent posture round her a little, perhaps continuing the soft call but sooner or later he adopts the stretch, which is silent. The female has probably been in the stretch all the time. If the male resumes the bent or walks towards a scrape to perform there he starts the soft call again. The female may follow him and may call when she scrapes. I have described the "successful" meeting of a pair. Often neither male nor female is so willing and both seem rather frightened of the other and the male often somewhat aggressive too. In this case both birds may adopt the slant or may make the bowing or scooping movement, both of which possibilities will be accompanied by the ky2 call. Brooding birds react to intruders at first by the keeyair or jik and if the other approaches closer by ky2 or tikitik. ~~Rikkixxxxxxx~~ If two birds both have strong territorial rights, a situation which doesn't develop until the eggs have been laid as a rule, both may adopt the Crouch towards one another, with the bill pointing slightly downwards, neck short, body often somewhat tilted forward. This posture may be accompanied by a twittering of the beak, apparently, ~~xxxxxx~~ when I have been able to hear it, produced by the Soft Call (which is in other situations friendly).

Now I am exhausted and you must tell me if there are further special points which need explaining.

You ask for a name for the Goethestellung. Goethe talked about it at the conference where he called it Herabstarren, which was translated as Staring Down, which seems a good enough name. My birds do it too but I haven't been able to do anything with it as it seems to be the intention movement of everything possible; ~~xxxxxx~~ in the gulls it may lead to pecking at the ground, picking up nest material sitting down, choking, pecking at the feet, bill cleaning and what have you!

I have written about the "postural facilitation" of displacement and other activities in my conference report. I was interested to hear of your many examples from the gulls. I was really concerned to show that not only may influences from

exteroreceptors ~~and~~ determine the activity but also, in some cases, proprioreceptors. There may of course also be proprioreceptive influences in some of the exteroceptive examples such as those you suggest about head flagging and preening the back.

About the manner of working of the proprioreceptive or exteroceptive influence I think it must be very much as you suggest. I suppose that when an animal performs an activity it has to overcome a certain inertia. Let us say that in order to feed it has first to go to a certain place and then to bend down and search in the ground for worms. One would expect that if it is already in the feeding place it will experience a stronger tendency to feed than if it first has to fly there. And in the same way if it is actually bending down close to the ground it may be more strongly aroused to feed than if it is standing up, (whether the influence is proprioreceptive or exteroceptive). As you say, this influence must be some kind of feed-back. So far so good. ~~Xxxxxxxthatx~~ But why should not the "extraneous activity" always occur whenever the particular posture is adopted. Does one in fact have to fall back on the idea of spark-over once again to explain this? I don't really know, but I ~~hope~~ not. Certainly I don't confine the idea of postural influence on subsequent activities to displacement activities. It has a much wider significance. For example I have seen in Eibl's hamster film how one of the hamsters made a typical back-stretching movement when the ben in the tunnel to its burrow made a sharp turn which so to speak started off the posture. Bill Verplank also told me that postural influences are important in maze-running in rats.

In short then it seems sure that ~~posturxxxxxxinfluencexxxxxx~~ a certain posture must increase the tendency of all acts (Russell et al. !) which have a similar posture. This increase in tendency must be some kind of feed-back process. Exactly how the tendency is increased I don't know. One situation where this ~~posturxxxxxxinfluencexxxxxx~~ postural influence may be important is in selecting displacement activities as suggested by Baerends (Tinberg, Derived Activities), and by Lorenz in same year (Proceedings of Deuts~~ch~~ Zoolog. Gesell.).

I wonder where you will be when this reaches you. We expect any day to hear any day that you have been expelled from some country or another as a counter-revolutionary - or elected as President. Fae told me you would kindly keep an eye open for any cormorant display. The sort of thing I am interested to know is whether the body is tilted forward in the advertising display, and especially details of any wing movements which may accompany the displays, and of course any fuller accounts of the movements themselves.

Your visit to the Noddies next year sounds most exciting. You certainly get around! I can hardly wait to hear about the nodding movement which sounds from Watson and Lashley's descriptions very similar to the bowing or scooping movement in the Arctic terns. Should it turn out to be a ~~new~~ hostile movement of this kind I would very much like to know if it appears in the pre-cop behaviour of the male. You remember that in the Arctic's precop it makes a little bowing movement which is rather like that during hostility though not ~~the~~ quite the same. However I have been driven to the conclusion that this movement in the precop is essentially the same, for the reason that it occurs only in those species where there is the hostile bowing display (Arctic and Common) and not in those which have no such display (Roseate, Sandwich, Caspian, Black).

I don't remember if, in my last letter, I thanked you for sending us a copy of your thesis, at last in print. We had referred so much to your thesis MS that it had become dog-eared in the extreme and it became almost impossible to find anything. Now we have already started dog-earing the printed copy!

Hoping to hear from you soon, if you can spare a moment from equestrian pursuits and mountaineering. I should be very grateful for anything to chew on, gulls, terns or cormorants.

Yours
Mike.

P.S. Have you seen Paludan's paper on the Kittiwake which is just out in Dansk. Før. Tidsskr., It tells some things but is very incomplete of course.

I have managed to get a microfilm of Hawkesley's thesis. Thanks for drawing my attention to it.

Dept of Zoology,

Oxford.

1 August

Dear Martin,

Now that the dust is beginning to settle I can once again take up my correspondence where I left it more than six months ago. I must admit that I am rather horrified to find your letter of January still unanswered and I will try now to rectify this error though you may have lost interest, or at least given up hope of getting a reply. In the accompanying sheets which you may be able to read, I have tried to answer your questions about which postures occur in which situations and which calls usually accompany them. I don't suppose it will be satisfactory for you - other people's replies never are - but it may give you some clue of the way I think things are. I trust that my nomenclature of the postures hasn't changed too drastically since I last wrote to you. I have regrettably abandoned "stretch" in favour of "erect" on the grounds that Palmer has used this name and furthermore that Baerends et al. in the Black Tern paper have also voted for it. "Slant" is an extremely unsatisfactory name for the rather vague posture which it describes but I haven't been able to invent a better, and I am afraid it may have to stick.

I imagine that all the "Thlasseus" terns will beg like the Sandwich but would be glad of any confirmation of this you could get. What is the begging of Anous like? I can't make much of Watson's description of the female tapping the male's bill.

By the way in his paper on Sterna eurygnatha I saw that Junge and Voous mentioned that they had received unpublished notes from Amadon on the comparative taxonomy of terns. Is someone about to publish something about this much neglected group? Particularly about the broader sub-divisions? and the relationship of the group with the gulls. Presumably "terns", even if polyphyletic, are derived from gull-like ancestors and have become more specialised for fish-eating, but I can't find even that much written down by a reputable taxonomist.

I append notes on your Extraneous Activities MS.

There is quite a lot of news from here but you will probably see Fae on her way west - or at least I gather there is a good chance - and will get it from her. The Hard Core is rapidly disintegrating and next year there will be noone left here except Margaret and us. One new man is coming, one Manley, and Niko talks about putting him at Ravenglass but we will try and save him from such an unkind fate. Uli is now an assistant lecturer at Birckbeck and David Blest, a later vintage than yours I think, is at UCL.* Desmond, as you will certainly have heard, is on commercial television and appears to be making a tremendous success of it - as you can imagine. They have managed to keep Ramona out for the time but we expect her to come on any day - ever since she got herself into the Womans Column in the Daily Telegraph as a competitor to Lottie Hass and Michaela Denise. Philip got his thesis in at the same time as I submitted mine and with the same hideous travail. Thank God I shall never have to do another. He (Philip) has a job at Edinburgh ~~in~~ as a Research Officer at a poultry research institute and hopes to astonish the world from there. We are all very glad that he has found himself a job. It was rather a worry. Rita's thesis is also in and she and Uli were at Ravenglass this summer. They concentrated mainly on pecking response work and tried ~~to~~ out some Lehrmanesque theories. ^{an} ^{Uli} ^{her} stuff on the control of egg-laying ^{which} is interesting but not really comparative ethology (though none the worse for that!). His work on the nest-building story, attempting to follow up your work, hasn't been very successful as far as I can make out. He ~~sat~~ removed one mate of a pair who were incubating and then sat by the other until it got tired and flew away, hoping to see and increase in nest-building before it did. But it apparently sat continuously (or almost so) for 48 hours without the least signs of become bored and it was Uli who first started displacement activities and gave up ~~first~~. He doesn't know if he will be able to go back there next year but I think he would like to go on with the pecking-response work if he

*Andrey in al **
Edinburgh

can get away from London.

I have temporarily turned from birds to fish and am rearing swordtails in isolation and under various experimental conditions, hoping to test their choice of mates when they are old enough to be interested in such things, i.e. when they are a few months old. Whether this will work or not I don't know but it seems that it should be ~~xxxxxx~~ possible and as the species is ~~highly~~ polymorphic (in domestication) one can try rearing one phase with individuals of another colour etc. It is all rather a business and ^{as they need to be treated} I always expect to electrocute myself on the tanks - a feat which Desmond once achieved, according to Fae. There is a chance that one may be able to imprint (at least in a related species) and if so it is a convenient animal because it breeds relatively early. Indeed this matter of early breeding was what decided us on working on this fish in the first place.

ever

Did you ~~xxxx~~ get the report on the conference from Frank ? You will probably have heard that Brenda has died so I don't like to write about the report at the moment. If you have had nothing from him I will send you my copy ~~xxxxxx~~ to look at and you can return it.

I gather from Fae that you are off on another trip around the New World and its neighbouring oceans. No chance I suppose of dropping in here. It can hardly be much out of your way.

All the best

Mike

P.S. Many thanks for the two Anuk papers.

chattering "tikitik..." call of Arctic, Common and Little. The latter species, however, have not organised the call into one of their normal ~~thkak~~ ground-threat displays (perhaps because they are more aerial than the other species and usually deliver attacks by flying at their opponents). The Roseate has an interesting type of gathering, very similar in form of movement, ~~x~~ as well as in call, to the Sandwich's, but it does not erect its feathers so much. It erects what it has of a crest but of course this is far shorter than the Sandwich and Caspian's, though longer than Common and Arctic. You mention "Rattling" in the Gull-billed T. Is this the call or the movement? Have you seen a gathering-like display in this species. I would be interested to know about the call which Jensen writes as "gorrok-gorrok". I imagine this is the normal call which is uttered when flying about with fish and on other occasions which corresponds to the "koreet" of the Sandwich, the "chorik" of the Roseate and the Fischruf of the Caspian. Is this your "Long Call Note"?

The existence of head-flagging and tilting in the Gull-billed is remarkable. I wonder what the situations are when they occur. The tilting seems to have a curious distribution as it occurs in Arctic and Common but I am pretty sure it is absent in the Roseate. In the Sandwich its place seems to be taken by a curious side-to-side swivelling of the head which v.d. Assem describes in his Lev. Natur paper and which he has amplified to me. However he has twice seen clear tilting (it happened to be the same individual on both occasions) in the same kind of situations. About other species I don't know except ~~xxxxxx~~^{and} the Black Tern, ~~which~~ appears to have swivelling like the Sandwich, and S. fuscata ~~which~~ tilting. Bergman swears that the Caspian has nothing of the kind, and he may be correct, though I would like to see the beast myself. B's film certainly didn't show anything very conspicuous but the species seems so similar in other ways to the Sandwich that I would search very hard for swivelling.

I am particularly interested in ~~many~~ the possibilities of using the food-begging behaviour of the young in assessing taxonomic relationships in the terns (and gulls?) and would be glad of any additional information which you don't publish about this, e.g. ~~but spp. were~~ if you arrive too late to make observations on pre-egg stage. In the 4 spp. I have looked at there are two kinds of f. begging: the Arctic/Common type which I think you know, with a series of single syllable uttered at each utterance and the Roseate/Sandwich type (also Caspian) with the calls uttered singly and accompanied by a slight head-tossing movement at each syllable, unlike the Arctic type. Is this head-tossing homologous with the head-tossing of the gulls when f. begging? If so is the food-begging of the Sandwich type more primitive than that of the Arctic? The Little Tern seems to have a totally different kind of food-begging with wings raised (Heinroth) and the Gull-billed also seems rather different from the species I know, as far as I can gather from the Johnny in the Carmargue.

I wonder how much you have done on the Noddyies - or contemplate doing. I have got an opportunity (still confidential of going to Ascension where I gather both A. minutus and A. stolidus live, as well as S. fuscata and Gygis. Do you think one could get anything out of these species in a year or less which you haven't yet picked up? Or do you plan to study one or more of these species in more detail? I may say that I am not terribly keen on this Ascension trip so that I shan't be upset if you are busy with ~~xxx~~ these species, but I would like to know what your plans are.

None of the Dutch people is working on the Gull-billed T so far as I know. There is a man in the Carmargue, name of ~~xxxxxx~~ who has been looking at something of their behaviour, mainly I think the way the young beg for food. He seems rather cranky, one of Portmann's people, and I don't think you will overlap much with him. Should you wish to get in touch with him his address is:

The Skimmer sounds a delightful creature. Perhaps I will one day hear about it too. Have you by the way sorted out the relation between the terns Erect and the gulls' Anx. Upright and managed to tidy away the Little Gull's Vertical?

Your remarks about recognising the Long Call were exactly what I wanted. If the Kittiwake Call and Moan of the Kittiwake pair off with Long Calls and "Muffled" Calls in the other species you have seen, I am convinced of their relationship.

origin

The terns all seem to have one ~~xxxxxxxxxx~~ elaborate call in their repertoire which is used in various male-advertisement ~~ceremonies~~ ^{displays}, as well as on other occasions. Judging from form alone one cannot see any relationship between this call in various species but I wonder if it may not have some common ~~xxxxxxxxxxxxxxxx~~ nevertheless. It is noteworthy that although the repertoire of Common and Arctic is so similar this call, the chief means I suppose by which an unmated male attracts a mate, is more different than any other, c.f. song of song-birds. I suppose the same kind of divergence would be expected in the Long Call if it also the "song".

Your analysis of the ontogeny of the various calls of gulls looks extremely useful and when one knows more of the development of terns one may perhaps link up the ~~xxxxxx~~ calls of the two groups using this as an additional argument. Here again I suspect you will be far ahead of me in homologising the voices of terns and gulls since your trips this year.

I don't remember if I wrote you before that I think the gakkerung of Sandwich, Roseate and Caspian Tern is homologous with the

| Black | Common & Arctic | Rosate | Sandwich | Caspian | Character of call | Situation |
|--------------|---|------------|-----------|---|--|--|
| "krerrr" | Kyō = Soft Call | "kurre" | "korrr" | "krerrr" | Soft, faintly, repeated irregularly | When pair close together: "greet", scapsg together, nest relief, etc. |
| ? | "kree yair" | Harsh Call | "waaaa" | "rrä!" (perhaps just higher intensity, greet) | Drawn out, wings in some spp. often raised | Rather strong alarm, commonest call when hargui over human predator in colony |
| keek | jik | chik | reet | "rä" | short, hard | Weak alarm call |
| "teek - ..." | "tikitik - ..." = Chatter | Gekkernig | Gekkernig | "kräh - ..." = gekkernig | a string of short hard syllables | Accompan a swooping attack on a ground predator, also by a bird in front v. another |
| "kree-a-rik" | "kitikeegeer" (Arctic) "keera" (Common) | Chorik | Koreet | Fischruf | Polysyllabic, the most complicated call in the bird's repertoire | Common call of intra-specific hostile encounters Also by birds carrying fish or advertising themselves as unmated. Typical of fish carriers but also occurs in fish flight & other performative ceremonies |
| "korrr" | Kyōw | | | rāu | loud, single, exclamatory | As an attack in driven tone, e.g. at lowest point of swoop v. predator, but also v. own sp. |
| "keew" | "Kreyer" | ?o | ? | rāu | colourless | Vague. "Contact call": Stimmlaufen |
| | "klii" | "keeo" | | | very musical | v. expressive, in Arctic often mixed with chatter. Unusual reaction to gall near colony |
| etc. | ♂ copulation call still "keer" | Food | Begging | | | |

Posture

Alert or alarm posture

Neck stretched forward & upward. (With ground
(~~object~~ & in air))
Wings often raised above back

Slant

Bowring

Crush

Approach posture or charge

(rare posture (dark) smooth like egg, upright)

Beat (with an iron & in air)

Silent or "jik" alarm call

"Kai" & "Keeyai"

} "kitkeeyer" call

Usually silent, I think, but sometimes a call heard indistinguishable from Soft Call (vid. inf.).

Silent

Soft call. (Agvavly "Kiyor yar yar kiyor kiyar....")

Silva

Scapulij

Black Hunched & Erect. Food Bagg.;

Aerial display

O's advertisement flight

In pass: bat 6ril

straight "

In high flight

A. ascent

B. glide

"kitkeeyey" call

soft call

silent (let in between passes sometimes food bags)

"jik" (= alarm call) & "klin" (= a pursuit call), the latter made by the bird who follows in the ascent.

The first bird who first swoop over the other may call "kitikeyer" but becomes silent for the pass. Otherwise calls as in the Pass. Occasionally the first swooper utters curious sequence of calls, "jik-jik-jik-jik..." in an accelerated pattern followed by slow "kyer-kyer..." This occurs ^{apparently} in purely hostile attacks but is rare at any time.

Aggressive calls in air

Diving swoop at another tern or at predator.

Familiar "tikitik... kyon"

Diving upward flutters

Sometimes a low "kuor", perhaps = kyon

N.B. Curious aggressive calls which are mentioned in "glide" which occasionally accompany an aggressive swoop.

(I think this covers most of the posture & call except for things like the ♂'s copulation call and a low intensity sort of call which I write a "keeyey".

Arctic
Tern.

- Low intensity dispute
- High intensity dispute
- Early pairing behavior
- Later pairing behavior
- Aggression

By thinking a predator is a
predator, it can not think "predator".

(-) indicates relatively less common than +

and any place where you have the
any way

My work on the behaviour of the Kittiwake is part of a programme of comparative studies on gull behaviour started by Dr. Tinbergen. It is planned to investigate the behaviour of all the species of gulls, skuas and terns possible. The work is mainly carried out in this country by Dr. Tinbergen and several of his students. But also in Germany, Holland, Finland and America people are contributing to it.

A study of one species alone is interesting in itself but only comparison gives access to many aspects of behaviour, for instance to the effect of habitat on behaviour, to the evolutionary origin and development of the more obscure postures, calls and ceremonies, and to the possible change of meaning and function of postures from species to species. The results of comparison can be of taxonomic interest as well. Two species, the Herring Gull and the Black-headed Gull have already been studied extensively, shorter studies have been carried out on the Common, Little, Laughing, Silver and Hartlaub's Gulls and we are at present going on several other species.

As all the European gulls only the Kittiwake does not belong to one of the two big groups, *Larus* and *Hydrocoloeus*; it is separated from the main groups on morphological grounds and forms an isolated genus *Rissa*. It also shows ecological peculiarities: it is pelagic and nests on vertical cliffs.

I have watched the birds only in the breeding colony and could not see much of their feeding habits and nothing of their behaviour in the winter quarters. Therefore I do not know how many special adaptations in behaviour they may have developed to a pelagic life. But tracking down their special adaptations in the nesting was one of the most fascinating parts of my work. In the following pages a number of these adaptations will be mentioned. Instead of pointing them out every time I will give a list of them at the end.

The islands of the Inner Farne are particularly well suited for this kind of work. They give unique opportunity to watch an undisturbed colony without a hide from the range and on a level with the nests. It is a great advantage to have an uninterrupted view over the whole scene so that one does not lose sight of the birds when they leave their nests. I did most of my watching in the early part of the stack. During 1953 and 1954 I kept the same group of birds under observation from the time of the birds' arrival in the first days of March up to the end of August when the young could fly. By the black markings on the wing tips, which vary individually but are constant in successive moults, I learnt to recognise the birds of this group of nests. Individual recognition was of enormous value in understanding the behaviour. It enabled me to follow up the history of the colony, to note individual variations in behaviour, and to recognise differences between new-comers and old inhabitants, between newly-mated and old pairs, etc.

In both years we saw the first kittiwakes at the beginning of March, a little time after we arrived on the island. They came to sit in groups on

the water in front of the breeding cliffs. Occasionally a bird started to swim towards another in an aggressive posture. The challenged one threatened back, others joined in, until there was quite an uproar from the flock which had been peacefully floating a few seconds before. But such outbreaks soon died down. Only once did I see two birds working up to a proper fight in this pre-nest stage, a striking difference to the picture a few days later on the cliffs. There was nothing to indicate that the birds were already paired at this time.

July 4th
B 49

A few days after the first group was seen on the water the birds started to visit the nesting ledges. In both years the same nest in my colony was occupied first, probably by the same individual (unfortunately I did not know the birds in the early days of the first season). At this stage the birds are very shy. They will not stay on their ledges for longer than a few minutes. In spite of that one can hardly fail to notice their visits; each time they will deposit a new white mark on the clean-washed rock. At the slightest provocation the birds will sweep out of the colony over the water as if in a panic, often manoeuvring in the air in a peculiar way: suddenly they throw themselves on one side, in this way changing direction, and swoop down rapidly some feet on the new course. After such a performance which I call evasive flight, the birds fly normally for a time but may repeat the evasive action soon afterwards. It is very likely that it is fear of the unfamiliar place as well as fear of ground predators which causes the kittiwakes to leave the ledges so often. But their special manoeuvres seem to be adapted against aerial predators. A chasing herring gull, for instance, is soon left behind; it is much too clumsy to follow the course of the kittiwake, which reminds one of the track of a doubling hare. There are other indications of the birds' fear of the land: they will not sit on top of the nesting cliff, nor collect on the preening places near the Churn as they do later. At this early stage they only land on the ledges and on the rocks below the cliffs. But after a few days the panics and evasive flights become rare, the birds stay on the nesting places much longer and stand about on the cliff tops. But the preening places on top of the island away from the colony are still not visited. In both years I noticed the first visits to these at the beginning of May. Both times they coincided with the start of gathering of nest material from the grassy top of the island. This is probably no coincidence. It seems rather that only the birds' strong urge to collect nest material can overcome their fear of the land. Only after they have landed there on their collecting trips do they dare to sit on the nearby rocks, but they always remain much shyer there than on the cliffs.

In the weeks which now follow pairing up takes place and a great amount of fighting, mainly in competition for nest sites. One's first season with a species is always specially fascinating as so many unexpected things happen. But my second summer with the kittiwakes was even more exciting because a great percentage of my old birds came back.

All the birds arrive unpaired in the colony. As a rule the males land first on the ledges and new pairs form in the following way. The males react as soon as they see birds circling in front of the cliffs, whether male or

at any distance?
Same reaction at all distances?

female, with a special posture and call (Figure 1). In this context the following features of the posture are important: the pointing down of the beak, the opening of the mouth and the lifting of the tongue. Further there is a rhythmic up-and-down jerking of the neck. A very similar posture has been found in all the other gull species studied so far and had been named 'Choking'. The circling females are attracted by this display and try to land beside the males. Repeatedly I saw how one female after the other visited a choking male, but none of them paid any attention to a non-displaying neighbour. If the inactive bird started to display then his efforts were soon rewarded as well. As this display with its call has a similar function to the song of some passerines, I will call it the kittiwake's "song". A male must be able to recognize a female's intention to land on his nest as his posture changes several seconds before she alights. He stretches his head towards the oncoming bird, opens the mouth even wider than before, flattens the tongue and gives a series of loud "kittiwake" calls. The female utters the same call while approaching. After she has alighted beside him the mutual kittiwake calling goes on for a few seconds. The male at the same time makes great efforts to face the female and to shout into her face. She on the other hand turns her head away from him. This often leads to a curious bowing and crossing of the necks. As the excitement dies down the female starts choking with one or two jerks downwards with open mouth, then she turns the beak up in the air, closing it at the same time, but still jerking until it is almost in a vertical position (Figure 2). After a few moments choking up the beak moves back into its resting position. The male goes on kittiwaking a bit longer than the female but soon after her he also performs the same choking display. This ceremony of kittiwaking, choking down and choking up I refer to as the "greeting". By the time the male finishes choking the female is already in a new posture, the broot, in which she still keeps her head turned away from him. He does not assume this posture. He just peers at her for a moment or two, as if he had to make up his mind, then suddenly he delivers a vicious peck at her. At this she usually flies away immediately. But if she stays he may peck her again; if she still doesn't go, he grabs her neck and holds it which has the desired effect. He may even hang on for a few seconds as she drags him into the air. In many cases she is pecked away in the middle of the greeting. He may even attack her before she has properly landed. There are considerable differences between the males: some peck every female as soon as she lands, others peck only hesitantly after a few minutes, some peck never at all. The females show an equal range of differences: some hardly put a foot on a nest, others endure the most vicious pecking. The females visit different males and the males receive different females. From very early on it is apparent that the females have preferences for particular groups of nests close together. They will visit them again and again. Often two or three males occupy the same nest in turn and the female who has a preference for the place will visit the same nest irrespective of the identity of the occupant. After a female has made a few visits to the same male he will gradually get used to her and tolerate her for longer until eventually he doesn't peck her any more. At this stage both will stay together on the nest for long spells, sometimes for hours, and there is quite a good chance of them pairing for the season. In many cases, however, such a relation gets broken up again but we will come to this later.

"attracted
right word?"

Please
drop word
"song"

long call?

found the
same in
both types
of chickling?

Wright?

Just as
Franklin.

I have mentioned earlier that a male recognizes a female's intention to land on his nest but if a bird prepares to land on a nest in the immediate vicinity of an unmated male he may mistake it and kittiwake loudly towards it as if it were a visiting female. But as soon as he understands the other bird's true intention his calling stops abruptly and he follows the "deceitful" animal with his eyes. Very quickly, however, neighbours learn to know one another individually and do not make mistakes each other for visiting females any more. Such incidents are wonderful opportunities for following the build-up of personal relationships between neighbours. Some examples of these social relationships are cited later.

*Wake "1
You're please
all need
Mar.*

I have said that a male reacts in a special way towards a female who visits him. Towards other birds, especially rival males, he reacts by another posture, the Arch and Bow (Fig. 3). As in the choking the mouth is open, the tongue protruded and a special call, the Moan, uttered. Birds who try to land on a ledge are often deflected away in the air when a neighbour starts to arch and bow or birds already alighted may take wing again as a reaction to it. This shows that the posture frightens or in other words that it has a "threat value".

So far only the function of some of the displays has been mentioned but we also want to know what causes the birds to show one posture rather than another. In some cases, as for instance in the Arch and Bow, it is not so difficult to assess the underlying drives. A bird so displaying often goes over to attacking an opponent but in some circumstances he may flee. Further he may show the intention of attacking and escaping alternately in quick succession. From this and other evidence one can conclude that in an arch-and-bowing bird attack and escape tendencies are awake simultaneously. If only one of the two drives was activated the bird would not display but act immediately, it would either attack or escape. The mutual interaction of the two gives rise to the display.

To analyse the choking display in this way is more difficult. I have to mention that the same choking (Fig. 1) which makes up the male's song is also shown during aggressive encounters between rivals. Like the arch and bow it can lead to attack or escape. For the same reasons we can presume that the attack and escape drives are both active. Can we now suppose that the choking of the male at flying birds and the mutual choking down of the pair in greeting has the same motivation? Let us first deal with the male: of his aggressiveness towards the female we see enough signs. His escape tendency also becomes apparent but only under special circumstances, but then it is unmistakeable. Attack and escape drives seem to be aroused in him. The female on the other hand shows her escape tendency clearly by fleeing. The fact that under exceptional conditions, however, she may attack the male gives evidence of her aggressiveness. One might expect that the sex drive must also be active in choking because choking is used in the mutual greeting and because in the song it attracts the female. But since choking occurs also in fights this is clearly not a necessary condition. The song of a number of species of birds, while attracting a female, seems to be motivated by a certain amount of aggressiveness and it is an expression of the female's sex drive that she

*Communication and
Aggressiveness
in animals
Volume 2*

approaches an aggressive male at all, but once the pair comes together in this way the choking seems to be the outcome of the same tendencies as in a fight. As one sees in many species how potential mates attack one another, whereas rivals show no sexual activity in aggressive encounters, the simplest hypothesis is that only the attack and escape drives need to be active for the occurrence of choking.

There remains still a question: why do the birds show different displays when the same drives are active? Moynihan suggests that the intensity level of each activated drive may vary independently and that the absolute level of each as well as the balance between them determines the postures. By applying several methods one can try to measure the absolute and relative strengths of the drives concerned. Moynihan has already made a careful analysis of the aggressive displays of the Blackheaded gull and it is part of my work to analyse the postures of the kittiwake in a similar way and to compare the results. The following observations show that there is a difference in the balance of attack and escape drives in the two postures, arch-and-bow and choking. If a contest between an arch-and-bow and a choking bird leads to a fight, it is the former who will attack first. If one of them escapes before it comes to blows, it is as a rule the choking one who retires. After a fight the winner often arch-and-bows and the loser chokes. From this one can conclude that in an arch-and-bowing bird aggressiveness is higher than escape drive and in a choking bird the reverse is true. It is more difficult to find the difference in the absolute intensity level of the drives in the two postures.

It is at first surprising that the females are attracted by aggressive behaviour in the males but it is significant that it is not the most aggressive posture which attracts them. The females would probably be too frightened to alight near a male who manifests the highest degree of rage. Moynihan found that in the blackheaded gull choking is far more aggressive than it is in the kittiwake. There is no doubt that the posture has a common origin in the ancestral form. But it appears to have developed in different directions so that in the blackheaded gull it is too aggressive to be used between the pair. The fact that a posture can change its motivation in the course of evolution is of theoretical importance.

Neither in the blackheaded gull nor in any other gull studied so far is choking known to have the function of attracting females. This shows that the functions of a posture can also change in evolution. It is already possible to make some attempt at an explanation of why the kittiwake can use the choking as song while other species cannot. Firstly in the ground nesting gulls the males often pair on "pre-territories" where the pair does not later nest, whereas the kittiwake sings on its nest. As we will see later, the choking is derived from nest building and it therefore might be expected that it occurs at potential nests. It may well be that such environmental influences have played a part in developing choking as song in the kittiwake. Secondly, in the kittiwake the females circle at the same level as the ledges, in the other species they fly above the males. This allows the kittiwakes to sing with the

*-Not necessarily
over/about? Big face?*

head pointing down as it is in the choking whereas the ground-nesting gulls have to point upwards, if only to see what is going on above. Thirdly the presentation of optical stimuli may also play a part in orientation. Just as different species have developed different movements so they have developed different structures. The brilliant orange of the kittiwakes' mouth and tongue is such a specialisation and since it is used so much in threat display it is probably a "threat structure". Also the yellow beak seems to have the same function. As I mentioned threat structures and movements serve to attract females. A kittiwake displaying on a ledge shows these structures to the birds flying on the same level even when it is pointing down. In the blackheaded gull the brown face, which is a threat structure, could only be seen by the females flying overhead if it were connected with a pointing up gesture, as indeed it is. Therefore it would seem likely that a ground-nesting gull which had evolved a special threat structure on its face would choke for song.

*Attitude that
starts fly
"overhead" ?
"all the" ?*

Having discussed the three main questions of causation, function and origin and shown how we can already begin to answer them for some of the postures, we will go back to the first meeting of the pair. We have seen that after the male's choking there is mutual kittiwaking and choking first down and then upwards and that the male is orientated towards the female while she turns away from him. The study of fights shows that kittiwaking is more aggressive than choking and one can understand that the approach of the female arouses the male's aggressiveness more strongly. I have mentioned already the female is also aggressive towards the male but her frequent flights show that she is more frightened than he is. This accounts for the fact that she turns her head away from him while he shouts at her. By this movement her beak is turned away, which is not only a preparation for escape but also hides her weapon and threat structures. She does well to do so as threat structures not only frighten another bird but may provoke attack, especially in the more aggressive of the two partners. Whether the presentation of the white neck actively inhibits attack is a question which cannot be solved without model tests, a technique difficult to use on cliffs. When attacked the young kittiwakes also show the head turning and display the black neck band towards the attacker. Here the black band seems more certainly to have an active attack-inhibiting effect.

*Not necessarily
over/about?*

A similar turning away movement was found in the blackheaded gull where both male and female use it in the greeting, it was called "head flagging" (after Noble and Burn). In that species the movements are much more sudden and "ritualized" than in the kittiwake. The ritualization is thought to be connected with the development of the brown face as a threat structure. Later on other species of gulls were found to possess the same movement in a form less ritualized than the blackheaded gull and more resembling the kittiwake. It seems typical of the greeting ceremonies of many birds that the initial postures are threatening but that they are followed by "appeasement" movements which tend to reduce the hostility of the mate. The "head flagging" of the black-headed gull just mentioned is such an appeasement gesture. In the kittiwake's the turning away of the female's beak certainly appeases the male but they have a further movement which both mates perform in the greeting which has much the same function, the Choking

What?
never

Up. In this the beak points upwards in a position from which the bird could not attack and the beak is closed so that the orange threatening inside of the mouth disappears. This posture never occurs in fights between rivals.

1. I have mentioned earlier that after several visits a bond may develop between a potential pair but may not last. The break is usually caused by the interference of other birds. In both years far more birds were in my colony than the restricted number of nest sites could carry. Very often a bird was chased from a nest by a rival and once he had lost his mate, more interested in the nest, abandoned him as well. Frequently the competing birds became involved in fierce fights. All the same I got the impression that at least all the males who wanted to breed could find a site to do so. The ones who were left over at the end were probably younger individuals (although in perfect adult plumage) who would not have produced young anyway. There was, for instance, a perfectly good nest in my colony which in the first few weeks of 1954, was always empty. Fierce fights were going on for all the ledges around but no bird bothered to occupy this nest. Eventually a young male appeared in the colony, occupied it and was hardly bothered by other birds. Had any of the left-over birds been serious about breeding they would probably have tried to occupy the nest earlier. Furthermore, I reckoned that there were still a few nesting ledges in the colony unused although at first sight every possible niche seemed to be occupied. It may seem surprising that it is always the young birds who lose in these fights but this has to do with the fact that the old inhabitants come back to the same nest each year and fight for the place with the greatest obstinacy. Often young birds usurp a nest in the owner's absence and I saw many of them defending their new conquests with great fervour but I only once saw one which was as persistent as the old owner. Even if the owner is beaten repeatedly he comes back to the nest again and again until he is able to defeat the intruder. The usurper, once defeated, does not as a rule come back any more. Once, however, in 1955, I witnessed the successful conquest of a nest. Funnily enough this did not occur at the beginning of the season but only at the end of May when the owners had already brooded their eggs for 9 days. The conquest was achieved by a pair, A, which owned a nearby ledge but had not attempted to build a nest on it. I had seen the birds standing together there for many days. Suddenly one morning the male A attacked the owner of the nest B. This led to one of the most vigorous fights I have ever seen. Both females joined in and often all four birds were packed together on the nest beating their wings and trying to bite each other. But four birds cannot stay on a nest for long. Soon they pushed each other over and tumbled down into the water. Usually the females gave up at this stage and flew away, but the males stayed locked together with their beaks and continued the fight on the water. They treated each other with fierce wing blows until one gave up and flew away. But a few minutes later all four set again on the nest and the struggle started anew. This went on for several hours; eventually the owner male, B, who was considerably smaller than the intruder, became exhausted and disappeared. Thereupon the intruders took possession of the nest but ignored the eggs which it contained. They stayed there the rest of the season without breeding. The beaten male came back only a day or two later and after a while he started to sing again on an unoccupied ledge which was so small that

2. *Conditioning*
3. *My trouble*

even a kittiwake would not be able to stick a nest on it. His old female did not come back to him; I lost track of her altogether so she probably didn't stay around the colony. He did not pair up again but was hanging about all the time. The following spring, 1954, the male B came back first to his old nest which he had lost the previous year. There he sang for a few days before male A arrived. One morning A was sitting on the nest when I arrived and male B had retired to the nest above. Although I missed the actual arrival of the new bird I doubt if there was any fighting again. From other evidence I know that the birds recognize each other and remember their acquaintances from one season to the next and a bird, once thoroughly beaten, will not dispute the claim of his conqueror. In the following days B occupied several nests in the vicinity of A in turn. But one after the other the owners of these nests came back and he was successively driven away from each till only the nest above A was left to him. Fortunately the owner of this one never came back so B could remain there and rear his young. A too produced offspring this year. B did not try to sit on his old nest any more after A's arrival, even when A was absent and the nest empty for long spells. He obviously knew that A might return at any moment. On the other hand he would not tolerate strangers on his old home. He threatened fiercely and even attacked them but as soon as A approached his courage wilted.

The female kittiwake comes back to her old nesting place just like the male. She may come back before or after him, sometimes days, sometimes weeks. If she comes sometime later, he has usually formed some bond with another female. If he is alone on the nest when she first arrives, everything goes well. They will greet each other with the usual ceremony and he will tolerate her beside him without pecking. As she seems only a little frightened of her old mate she will often stay with him for a long time, sometimes for hours. But the arrival of the old mate does not stop the new female visiting the male and sooner or later the two females will meet on the nest. This is often the start of a long and bitter combat. Each of the females tries desperately to cling on to the ledge at the same time trying to throw off the rival. Sometimes they both maintain their position for half an hour or so. The ~~male~~ also joins the fight and pecks each of the two in turn. Usually the new female is first to leave. Only once did I see how the old one was thrown off and did not dare to come back for the day but the following day she tried again and then she was victorious. If the female comes back to the colony before the male she usually visits several males in turn but always comes back to her old ledge in between. She defends her nesting place but as females do not fight as fiercely as males she is often thrown off by a male intruder. But there is an easy solution to this one. When the intruder starts to sing on her nest she simply visits him. When her old mate comes back the intruder is thrown off anyway and the pair reunite. It has, of course, survival value for the species that the birds pair up with strangers if the old mate is absent. The old partner may have died in winter and in this eventuality the stranger takes his or her place.

I saw one specially clear case of personal recognition between old mates. The female, who was a particularly shy bird, came back before her mate of the previous year. She visited a few males in the neighbourhood but never stayed

any time with them. Then she left the colony for a few days as individuals often do at this season. During her absence her mate arrived and started to sing. He was a strong and beautiful bird and sang more intensely than most of the others. He was very successful^{too} and one female after the other visited him but he pecked them all away, usually even before the greeting ceremony had ended. This went on for a couple of days until his old mate came back. The first day of their meeting they stood beside each other on the nest for half the day without a trace of pecking.

The neighbouring male took a particular interest in this female. The two nests were on the same long ledge and very often when the female was alone he walked over to her leaving his own mate behind. As he never took the slightest interest in the female of his neighbour on the other side, whom he could reach just as easily, one can conclude that he had a special affection for her. His interest in her as just as lively in 1954 as in the previous year.

As the season advances the mates begin to show more and more sexual behaviour. The female frequently begs for food from the male and he responds by feeding her. Very often copulation takes place immediately afterwards. The food-begging of all species of gulls is similar but the ground-nesters open their beak every time when uttering the call, while the kittiwake holds its beak firmly closed. As food-begging is a sexual, non-aggressive display the kittiwake cannot afford to show its bright gape, the structure which seems to release fear and hostility in another. An interesting point in the courtship feeding is that the kittiwake male feeds the female from the throat in exactly the same way as he feeds the young. The ground-nesting species differ from the kittiwake in this respect. They push the food into the beak-tip and present it thus or they let it fall to the ground where it is picked up by the young or mate. It is of theoretical importance that each species uses the same pattern in feeding the young as in courtship feeding. The difference in the feeding methods is probably connected with the fact that the kittiwake-chicks are bound to stay at their nests whereas the young ground-nesters can rove about and be fed somewhere else. Half-digested food cannot always be picked up completely and it is very likely that soon a little heap of rotting food would collect in a kittiwake's nest if the birds fed in the ground-nesters' way. This would not only smear the young but it might also develop into a seat of disease. That it is important for the kittiwake to have a clean nest is shown by the fact that this species has a special nest-cleaning reaction which is absent in the ground-nesters. All the birds, adult and young, will immediately peck up any strange object which falls into the nest and fling it far from the ledge with a vigorous head-shake.

At the beginning of May the birds start to build their nests. Often quite a lot of pairs suddenly start to build simultaneously, keep it up for a couple of hours and gradually lose interest at about the same time. One morning one sees the birds busily flying to and fro so that the colony is as busy as a bee-hive and in the afternoon all of them stand dully on their ledges as if they had never been interested in nest material. They collect the

Induction

material in groups together from several places on the grassy top of the island and on the exposed screeed. Often I saw from the window of the Tower how the sight of one bird alighted encouraged the others flying above to land beside him, so that in no time a group had assembled. The birds of such a party would leave the place all together. The latecomers who often had no time to collect material always took wing with the others "empty-handed". They were apparently too frightened to stay longer. It was striking how the birds on their way home flew straight towards the sea by the shortest route, irrespective of the direction of their nest. To reach their colony they often had to fly quite a long way round the island afterwards. Travelling over land is done by a kittiwake as little as possible. I never once saw a bird flying over the island until the start of nest building. The kittiwake is the only species of gull which is known to collect nest material in groups. The other gulls set off on their collecting trips independently from their neighbours. They do not seem to have such mass outbreaks of building activity. The ground-nesting species collect the material either in the breeding colony or in an environment similar to where they nest. The kittiwake has to leave its familiar ledges and land on exposed flat ground. One can therefore understand the kittiwake's greater reluctance to collect alone and only the security of the flock seems to overcome this inhibition. As in many birds, the flocks seem to offer protection from predators. The guarantee that the birds collect simultaneously is given by the mutual stimulation to build. The sudden outbreaks of building activity in a kittiwake colony are therefore not happening by chance, they are connected with other adaptive measures which all help in the survival of the species.

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pairs I had under observation, inexperienced birds which had not bred the previous year, built half a nest three times in succession and every time it fell down into the water. After the third attempt had failed both, presumably fed up with the business, left the colony together. This is a very unusual thing for a pair to do in the building phase. After two days, however, both returned, had another try and succeeded. Such incidents, although interesting in themselves, do not make the collecting of data very easy.

Soon after the nest is finished the eggs are laid, in the middle of May. The clutch size is usually two, often only one and in some cases three. The ground-nesters mostly lay three and one wonders why the kittiwake is again an exception. The following observations may give a clue: of five pairs with three eggs which I found on Inner Farne this year, not a single one was able to rear three young. I witnessed in two cases how one chick was accidentally knocked off the nest by a parent. In the other cases I found that a young had died or disappeared without trace. Such accidents also happened to smaller broods but there they were rarer. It may well be that the nest is really too small for three young. The fact that it has to be stuck on small ledges limits its size of course, but I do not know whether it is relatively smaller than in other gulls. Furthermore, it is possible that the kittiwakes, being a specialized feeder on fish, does not find enough food for so many young as easily as the gorging gulls.

From the first egg on the parents brood in turn for 27 to 28 days until the young hatch. The question of the recognition of young by their parents and by their brothers and sisters is dealt with afterwards. The chicks stay in the nest for 6 to 7 weeks during which time they have to confine their activities to a compass of a few inches. It is hardly surprising therefore that their first flight is a very exciting affair and takes long preparation. A chick near to flying will flap its wings for a minute or two, always facing the wall. Suddenly it will jerk its head round as if it was going to jump out at any moment. But soon it turns back towards the wall again and after a while starts another flapping bout. Time after time it comes closer and closer to flying and the suspense becomes almost intolerable for the observer - to say nothing of what it must be like for the chick. The bird even begins to flick out its wings in preparation for flight but again and again it comes to nothing until suddenly it leaps out into space for the first time in its life. The first flight is astonishingly competent though without the dexterity of the adults and during the next few days it quickly improves.

For the next week or two the young come back to the nest to be fed by their parents. The rest of the time they spend on the preening rocks or floating in the water. I do not think the young birds feed themselves at this age. One only very rarely sees a young of the year fishing near the island. Often at this time flocks of up to 50 fledged young assemble, accompanied by only one or two adult birds. This suggests that the young attract each other in some way. It may be that their very distinct wing pattern serves as a signal. About two or three weeks after the fledging of most of the young the chick

groups suddenly disappeared. The younger chicks still remained but the main body had gone, obviously by themselves as their parents were still to be seen on their nests up to the end of my time on the island.

The next few pages contain a more detailed discussion of some points which would have been out of place in the main description.

Method of Recognition of Individuals.

With some practice it is possible to recognize the individuals of a kittiwake colony by the black marks on the 6th primary. Figure 6 shows that the dark pigment^{ed} area gradually decreases from the second to the sixth primary. Such gradual changes through series of adjacent feathers are common features in the plumage of birds. They can be observed in different parts of the body and can affect many different properties of the feathers apart from pigmentation. In one feather row the same change can progress in different directions, as in Franklin's Gull in Fig. 7 where the dark area decreases from the 4th primary on either side. The greatest variability is found where the pigmentation tails off. This is also shown in Fig. 7. The pattern of the 6th primary in the kittiwake shows about the same range of individual variability (Fig. 8). It is very fortunate that the tip of this variable feather is clearly visible in the kittiwake when the wing is folded. In most of the gulls, as for instance, the herring and black-headed gulls, the pigmented area extends further back in the row of primaries so that the favourable region is always hidden in the folded wing (Figs. 4 and 5). Another fortunate chance is that the pattern, however variable from one individual to another, is fairly fixed in the same individual and comes out after the moult almost exactly as it was before. In 1934 I was able to follow one of the old inhabitants of my colony right through the moult in the autumn. Its successive patterns are shown on Fig. 8. The wing feathers are only moulted once a year by the adults, in autumn, and abrasion hardly affects the black areas until a few weeks before the feathers drop out, although the light areas which are less resistant become badly worn.

There were, however, individuals with patterns which I could not distinguish from each other but mostly I was able to keep them apart by differences in other characters such as beak or leg colour, or by voice or behaviour, all properties which persisted from one year to the next. To give an idea of some behavioural peculiarities I might mention the attachment of a bird to his neighbour's female, the building of a gigantic nest or an unusual rhythm in one of the calls.

By using all the different individual characters there was little doubt about the identity of my birds through the season and in the successive years. But since so much of my study has turned on the recognition of individuals I hope to accumulate further evidence next year on the constancy of wing markings and other characters.

Chick Recognition.

Dr. Tinbergen found by experiment that herring gulls do not recognize their own young in the first days of the chick's life. They only learn to distinguish them individually^{after} about 5 days. But they never learn to distinguish their own eggs from those of their neighbours, sometimes quite a different colour. They rarely recognize the locality of their nest site. These two types of recognition are well adapted to the behaviour of eggs and chicks: the eggs remain in the nest but the chicks soon start to run about. The personal recognition guarantees that the parents feed their own young. If one assumes that the parents learn to recognize the chicks for this purpose,

one would expect that the kittiwakes do not need to distinguish them as their young are nearly always tied to the nest until they ^{can} fly.

I made a number of experiments to find out if the kittiwake's behaviour agreed with expectation. Young of different nests had to be exchanged, a not very easy task as few nests are accessible on the Inner Farne. Most of the tests had to be carried out on the Staples. We had to visit that island a number of times merely for establishing the age of the young. But the weather did not allow us to cross as often as we wanted at the time of hatching and in order to find more exactly the age of the chicks, I measured daily six young of known age on the Inner Farne. I made several different types of measurement on each chick and found that the length of the "hank" was the one which was the most accurate indication of age (Fig. 9).

In all the tests the young were left in the strange nests for 5 minutes or longer. In the first series of experiments I exchanged broods of the same age and the same number of chicks. All the young were accepted, that means that the parents showed the same behaviour to them as to their own young, which varies with the age of the chicks. Small young are brooded, larger ones just guarded. Sometimes a young is preened a little or even fed. The number tested in each age group is shown in the table.

| Age in days | Age Group | No. of tests |
|-------------|-----------|--------------|
| 0-6 | 1 | 7 |
| 7-13 | 2 | 9 |
| 14-20 | 3 | 14 |
| 21-27 | 4 | 6 |
| 28-34 | 5 | 1 |

Some observations.
Older young get more difficult to handle which is why I made fewer tests with them. As I could not test the oldest young I cannot exclude the possibility that the parents might learn to recognize their chicks later. I have, however, indications that they do not as a rule. After the chicks could fly (around 45 days) I saw several times how parents accepted and even fed newly fledged strangers which had landed on the wrong nest. In a few cases, however, a strange fledgling was pecked away. The variable behaviour of the parents may be due to the fact that the strange chicks behaved differently, but such visits are too rare to decide what is typical.

The next experiments show that the parents do not recognize their young by their state of development, a possibility not excluded by the previous tests. The "own brood" were replaced by another of the same number of young or eggs but of a different age. All were accepted.

| No. of individuals in each brood | Age Group of Own Brood | Age Group of Replacing Brood |
|--|---------------------------|---------------------------------|
| 1 | Pipped egg | 2 |
| 2 | Eggs near hatching | 2 |
| 1 | 1 | 2 |
| 1 | 1 | 2 |
| 1 | 1 | 4 |
| 2 | 1-2 | 4 |
| 2 | 2 | 1 |
| 1 | 4 | 1 |
| 2 | 4 | 1-2 |
| 2 | 4 | 1 |

I left a few chicks exchanged after the tests.

2 young of age group 2 were left exchanged with 2 young of age group 1.
1 " " " 1 was " " " 1 " " " 1.

All four broods were reared by the foster parents.

So far the experiments have only tested the reaction of adults to strange chicks. The behaviour of the chicks themselves to strange nestmates is also peculiar. In a brood of 2 young of the 4th age group, one chick was replaced by a stranger of the same age. The strange chick was slightly bigger than the remaining young. As usual the parent accepted the new bird but the chicks did not get on together. At first both young crouched for a couple of minutes. Then the owner chick lifted its head at which the stranger grabbed its beak viciously in a clearly aggressive manner. At once the owner young turned its head away from the stranger and the attack stopped. But it started again as soon as the owner lifted its head. The parent paid no attention to the quarreling young. A few more experiments which were made for a different reason also suggest that chicks know their brothers and sisters. It was always the larger young who would attack the smaller, whether he was in his own nest or not. I do not know at what age this hostility appears as no experiments for this purpose were made. The youngest chicks in which I saw it were 9 days old. Twice I observed how a three day old chick wandered into a strange nest and was accepted by the occupying chicks who were then under seven days old. This suggests that the young learn to recognize each other when they are about a week old.

72? It is difficult to imagine what function this recognition may have, especially as the adults have lost it in evolution. I can only suggest that it may be important in competition over food. Brood sisters who sit in peace together half the day will suddenly start to quarrel when the food comes. In a brood of two young both chicks, standing on either side of the parent, are equally close to the parent's beak, but the larger young increases its chance of getting the food by pecking at its smaller nest mate. One vicious peck at the beak or into the face suffices and the smaller young

all Juvally tree of
all Juvally tree of

will swivel its head violently away from the attacker so as to hide its face. In this position it will stay for a few seconds or longer and this posture seems to stop the attack. But as soon as the chick turns back it gets another peck and its head jerks round again. This is often repeated several times. Frequently the parent starts to feed the larger young while the smaller one has its head turned away. The smaller chick watches the parent's beak carefully from the corner of its eye and as soon as the food comes up its beak shoots into the parent's mouth, but as a rule the larger chick gets most of the meal. Luckily the parent usually procures so much food that the older young is satisfied before the supply stops so that the younger one gets a chance as well. In times of food shortage the older chick would certainly get all the food and the smaller one would perish. This is more advantageous for the survival of the species than half-hearted feeding of both chicks. A few of my observations indicate that as one might expect, the larger chick pecked the smaller one less often in well-fed broods than in badly attended ones. In a few nests one of the chicks died before it could fly and it was always the youngest. I could not decide how much food shortage and food fighting were responsible and a careful study of this point alone would be rewarding.

*"in its nest attitude
"inhibit" own
small chicks
never defend them
never attack by large
birds*

I have mentioned that the attacker stops pecking as soon as the opponent hides his face. This inhibition of aggressiveness is probably reinforced by a special structure, the black neck band. Of all the juvenile gulls, only the ^{young} kittiwake has developed it. A chick which turns its head away from its opponent thereby presents its neck-band and displays it further by erecting the neck feathers, (Fig. 10). The comparison with other gulls shows that the feathers bearing this black band develop precociously. The band is displayed as if it were intended to inhibit attack and I have direct evidence that this happens. From what takes place in fighting in adult kittiwakes, in ground-nesting gulls and in other birds, it is surprising that contests between the chicks are so short and that the attacked immediately turns his head away and never tries to defend himself by pecking back. The young kittiwake seems to have developed all these specialisations to secure a quick decision in aggressive encounters between brood mates. One can well imagine that a prolonged fight on such a small ledge might be disastrous for all the contestants. In addition most birds when defeated can still resort to running or flying away, an alternative which is denied to the young kittiwake.

*But rare
attacks by adult
much more
dangerous*

If a young gets pecked by an adult it turns its head away from the attacker as well and the adult also stops pecking. I thought at first that the reason for the development of the black band might be the need for an inhibitor of the attacks of strange adults. But the parents guard the nest and young so well that encounters between young on their nests and strange adults are far rarer than food contests between brood sisters. Therefore I am now inclined to believe that the black band has developed in connection with intra-brood relations.

As I have mentioned earlier, the adult females also show the same head

turning on the young when they are likely to be pecked. There too it may stop an attack. It is extremely difficult to compare the effectiveness of the adult's white neck with the chick's black band as they are never shown in comparable situations, but I hope to get more information about this problem next year by some tests with models of kittiwake heads.

Some Adaptations of the Kittiwake
to cliffnesting compared with

Since the territory consists only of a small ledge, most fights start on ledges. The birds attack mainly by grabbing each other's beak and then twisting head.

With specialisation to fighting by grasping beaks are probably connected:

Yellow beak strong attack-releasing stimulus.

Beak hidden in breast feathers in an appeasement.

Beak of the Young pitchblack, of a distinct colour, seems not to be just immature colouring, beak of young must probably resemble as little as possible that of adult.

Inside of mouth and tongue brightly coloured, shown in all threat-postures and hidden in appeasement and sexual postures such as foodbegging.

To summarize: important optical stimuli concentrated on beak and mouth.

Choking as song.

Contact not absolute

A bird performing the aerial threat-display describes roughly a half circle in front of the cliffs. It achieves this course by changing its direction regularly in one phase of the display.

Social collecting of nest-material.

Mud as nest-material.

ground-nesting Gulls (based mainly on the Herring Gull and Blackheaded Gull).

The territory is larger. In fights the birds try to get on top of opponent and peck down or to grab any part of him and pull backwards.

Beak does not release attack so strongly.

Beak only turned away from opponent in appeasement, not hidden.

Beak of Young dark brown or blackish with pinkish patch at tip, colour seems not to be specialized.

Inside of mouth may be brightly coloured, tongue seems not to be. Mouth open in some, but not all threatpostures, tongue never lifted and displayed. Mouth not closed in foodbegging when uttering call.

→ "ditto" to some extent

Choking not song.

In the aerial display the birds fly in a more or less straight line over the colony.

Contact not absolute

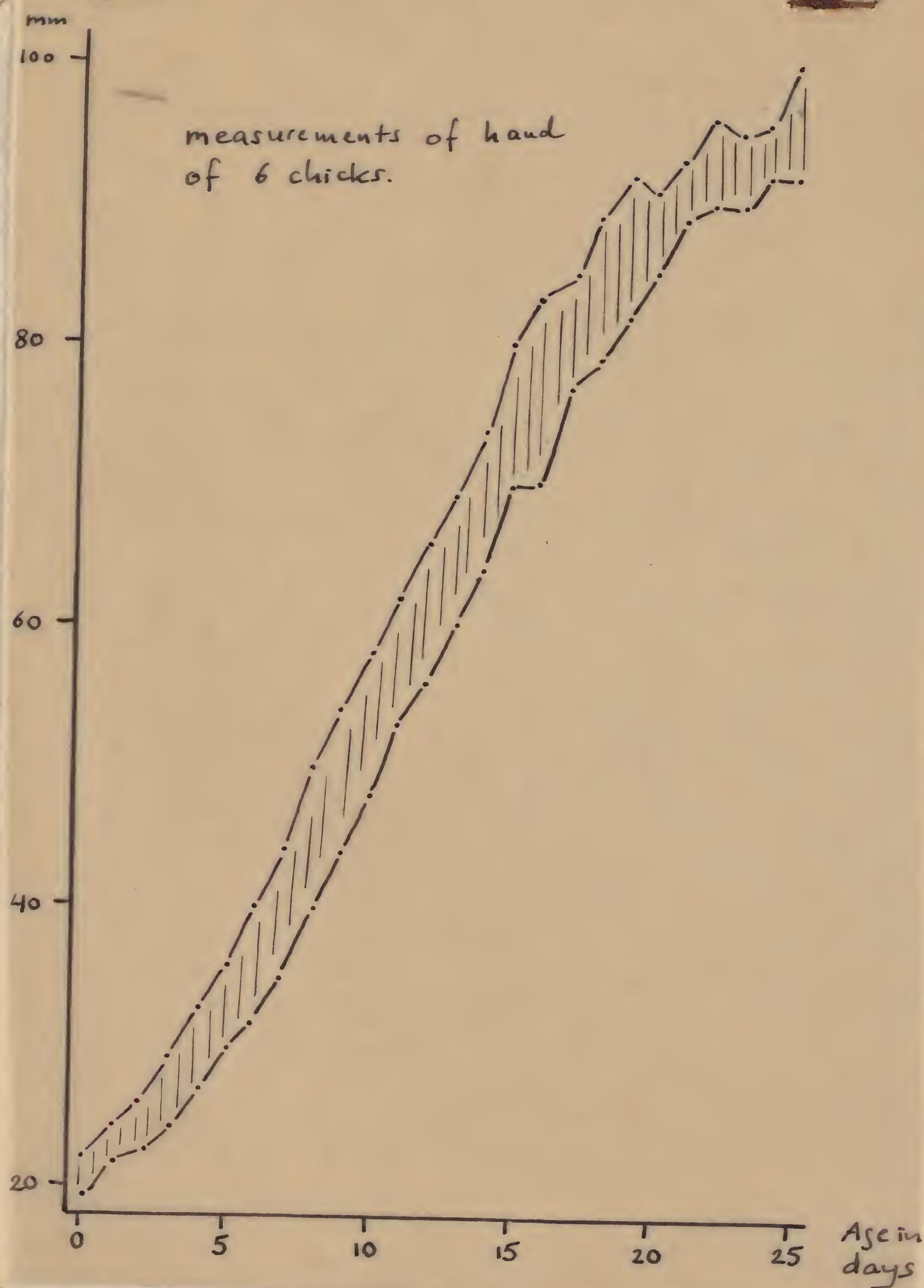
The individuals collect alone.
Some nuances

Only reeds, dry grass etc.

Water plants also

| | |
|--|---|
| Prolonged paddling on nest-material. | Only traces of paddling. |
| Pairs don't leave nest alone after start of building. | Pairs leave nest alone until first egg is laid. <i>Not necessarily</i> . |
| Small number of eggs (1-2, 3 exceptional). | 3 eggs. <i>Very dependent upon young.</i> |
| Eggshells not carried away. | Eggshells carried away. |
| Young: not cryptic. Mostly stand with face towards wall, don't move about. | Young: cryptic (hide under cover from predators). walk off nest shortly after hatching. |
| Start wingflapping several days after hatching. | Start wingflapping shortly after hatching. |
| Squirt droppings under pressure over nestrim. | Produce droppings with much less pressure. |
| Have black neckband. Neckfeathers develop precociously. Have headturning and appropriate behaviour of attacker. | Have no neckband. ???. Neckfeathers develop later. Have no headturning. <i>Have analogues</i> |
| Parents: have no feeding call. | Parents: have feeding call. (probably for attracting young to feeding place). <i>Not necessary</i> |
| Feed young from throat. Don't recognize young. | Feed young from beaktip or ground. Recognize young after about 5 days (in Herring Gull). |
| Young and Adult: have nestcleaning movement. Have sharp claws and strong toes adapted for holding on ledges. Are extremely tame on cliff (but not on top). | Young and Adult: have no nestcleaning movement. Can't hold on ledges so well. Are always much shyer. <i>Apparently depends upon experience</i> |

FIG. 9



The graph shows the max. & min. value for each day.

Murch.

Some Aspects of the Behaviour of the Shag.

1. General.

During 1953 and 1954 I watched the behaviour of shags during the months of March and April. Most of the observations were made at the nesting cliffs but the point of observation in 1953 was in full view of rocks at the foot of the cliffs where the birds used to collect to preen and sleep when the rocks were uncovered by the tide. I found that all the courtship behaviour might take place on the preening rocks though less commonly than on the nests. In 1953 most of the observations were made at the nesting cliffs near the Stack, especially on one cliff where three pairs finally reared young, but in 1954 this cliff was less interesting and I watched instead at a place on the north-west of the island where two pairs reared young. In addition to the pairs which nested successfully there were always several other pairs which went through the courtship phase and even attempted to build a nest. There were also unmated birds who regularly tried to occupy ledges or find mates.

It was soon very clear how important it would be if the individuals could be recognised and I found that the pattern of dark and light flecks on the yellow and black area at the base of the mouth could often be used. There were other small characters of the plumage which were also sometimes useful and in this way the identity of certain individuals could be established. Some individuals were already ringed and in 1953 two males were colour ringed with chicken rings. One of the colour ringed birds had a rather striking and unusual yellow patch and the ringing confirmed that he retained this feature in the following year. It should be mentioned that as the season advances the outlines of the yellow patch of the adults becomes dulled and the yellow colour begins to spread along the lower mandible until the winter condition is reached. Then in the winter or early spring the yellow recedes till it occupies, viewed from the outside, only the area around the base of the mouth. The new pairs form in the early part of the spring when the yellow patch is most striking and the crest is best developed. Even before incubation begins both have become less impressive. In just the same way the white flank patches of the Cormorant, which seem to be used in pair formation, often disappear by the time the eggs are laid.

I collected notes on the relation between the plumage of birds and the interest they took in reproductive affairs. They showed that the earliest birds to come into breeding condition were those showing most completely the adult characters. A little later one saw other birds beginning who still retained a trace of brownish on the chin or yellowing of the lower mandible

or had a poorly developed crest. Sometimes, when these "pre-adults" visited a ledge regularly, I could see that the yellowish on the bill gradually disappeared over a few weeks until the adult condition was reached. According to Witherby the adult plumage is acquired only when the bird is about 3½ years old. Since most breeding shags are in adult plumage they must normally breed for the first time when nearly three years old. But there is often considerable disagreement between the acquisition of the adult feathering and the adult condition of the "soft parts". The distribution of yellow on the lower mandible and around the mouth is particularly important and such characters are notoriously difficult to assess in museum material. The age of sexual maturity probably varies quite a lot. One male who nested rather late in 1954 had a yellow patch which was adult, immature leg colour and feathering which, according to Witherby, would suggest he was about one year old. A thorough re-examination with parallel field observations would be well worthwhile.

In addition to individual differences, it was fairly easy to distinguish differences between the sexes in the adults. This was most clear in the behaviour but expressed itself also in the size, development of the crest, etc., and especially in the voice. While the males possess an impressive, if not very beautiful, voice, the females in the breeding season can only make an ineffective huffing. In some of the earlier descriptions of shag and cormorant behaviour the identity of the sexes has been confused.

The displays of the shag do not seem to have been described beyond a few noted by Selous in 1901 and 1927. This is the more surprising as the behaviour is quite common and shows a number of peculiar features. One of the more remarkable is that in addition to normal mountings to copulate the female may mount the male using exactly the same gestures with which he prefaches his mountings. These reverse copulations have largely led to the confusion in identifying the sexes and are responsible for the statement that the females are more active in the display than the males.

A further reason for studying the shag was that it is a relative of the cormorant, a species which has been studied by Kortlandt and whose behaviour is probably better known than any other bird's. However Kortlandt's interpretation of the displays is somewhat at variance with ideas based on other animals and in particular he seemed to overlook the aggressive element in courtship. It seemed useful therefore to examine another member of the cormorant family to assess the limitations of the various theories. The main object of my study was the reproductive behaviour, especially territorial defence, pair formation, copulation and nest building. In both years my observations were broken off at the beginning of May soon after

the eggs were laid because of the arrival of the terns, the main object of my visit to the island.

I had hoped to collect more general observations on the breeding biology of the shags, such as the interval between laying successive eggs, the periods of incubation and fledging. This turned out to be more difficult than I had expected and I soon stopped trying because the shags can be close sitters on their eggs or young and herring gulls became too interested in my activities. Notwithstanding, clutches disappeared in both years. Part of the losses ~~was~~ was due to a heavy southerly swell at the same time as a spring tide, a coincidence which occurred in both years. Each time we watched helplessly as one of the lowest nests was washed off, in the first year when it had eggs, in the second year just after the young had hatched. A few of the nests near the top of the cliffs also suffered from egg-stealing. In the one or two cases where there was relaying I could never be sure that it was the same pair. The rearing of the young is so lengthy a business that there is no question of a second brood following the successful raising of the first. (At one nest it was 92 days between the laying of the first egg and the flying of the young.) Further the young continue to be fed on the water and ashore even after they can fly.

Since only a few nests could be kept under day to day observation as was necessary, my observations in each year were based mainly on rather few individuals, probably not more than 20 principal characters in all. These birds showed considerable individual variation in character but it was generally possible to disentangle what was typical for the species and what was the idiosyncrasy of the individual. But some such inaccuracy may have crept in. In any case I have tried to avoid using the words "never" and "always".

When we arrived at the beginning of March the shags were hardly interested in their nesting ledges and there was little other signs of reproductive activity. In the next week or two they spent more and more time at the ledges and for a few hours in the mornings and evenings they might show a certain amount of display, punctuated with long periods when they sat inactively.

At the time of our arrival most of the shags on the island were apparently roosting on the Megstone. They were absent at night but returned in the morning before it was light. Those who were most advanced would visit their ledges for perhaps half an hour or so and then would leave and not return to them again until the evening. As it became dark all the birds around the island would fly off in ones and twos and could, under favourable conditions, be followed until they landed on the Megstone. This evening flight from the Farne enabled one to discover how fast

the birds travelled, as they flew in a purposeful way straight to the other island. The distance from the north-east corner of the Farne to the main roost is about 1 mile 110 yards. Nine flights in all were timed on two different days and the time taken to cover the distance varied between 1:30 and 1:12 seconds. The average speed for the nine flights was 36½ m.p.h. On both evenings there was only a very light southerly wind so that the actual air-speed was probably about 30 m.p.h.

As the season advanced the time the last bird left a particular group of nests became later and later in relation to sunset as well as to actual time. By the fourth week in March some birds were spending the nights at the cliffs and these individuals were those whose breeding cycles were most advanced. But there were still some nights when no birds roosted at the colony. The morning attendance was much more regular than the evening and some pairs could hardly be said to make evening visits at all.

From the beginning of the season a few birds behaved as if they were already paired and nearly always stood together on a particular ledge. It was probably significant that these well-paired birds were on the "best" ledges. However most of the birds did not give the impression of being definitely paired to a particular individual although from the earliest they might show some slight preference. The males who were not paired would spend long inactive periods on a chosen ledge, which were interrupted for bouts of advertising display towards female shags who came near. The male attracts females with this display. Some of them he pecks away, others he accepts for a time but then pecks them away. Gradually he establishes a preference for one and will peck away all the others who come to him. Another change also takes place. In the first days as soon as a female left the male he started once again to advertise. Later this becomes less and less likely and as a result he is visited less and less by strange females. A discussion of the details of the motivation, function and origin of the male's advertising postures will be deferred till later.

Whenever the rightful female returns to her mate they show a "greeting" display which develops out of the more or less hostile manner with which the unmated male received a female. The most important feature of this greeting is the appeasing Upward Gape display which both birds now give, not merely the arriving one as occurred earlier. This is important as showing that the bird on the ledge is no longer so hostile to the approach of its mate. When the female is at the ledge and the male alights there, there is the same greeting. This regular greeting at the return of the mate to the nest causes one to forget that the pair may still be slightly hostile to one another. This is however shown by such observations as the following. One day there was a strong wind blowing on to the cliff where I was

watching, which caused all the shags difficulty in landing. A female was alone on the ledge when her mate came in to alight but his touch-down was rather unbalanced owing to some slight eddy. At once his mate pecked at him and he fell off and had to circle once more. This time his approach and landing were faultless and there was the normal greeting exactly as if there had been no hostility at all between them. Further evidence that the mates can still be hostile towards one another is shown by the fact that after a male has driven an intruder from his territory, he may be so enraged that he even attacks his own mate. Indeed there are indications that far from a decrease in aggressiveness the female's initial fear of the male is replaced by a slight aggressiveness towards him by the time the eggs are laid.

When another shag lands near the ledge where a male has his territory he threatens the arrival using one of several postures. If the arrival is a regular occupant of the ledge the threatening may die down quickly, but if it is a stranger the threatening male may launch an attack on the ledge if it is within hopping distance of his own. Such observations as these show that not only do the birds learn to recognise their mates but they also know the other habitués of the colony. I have not been able to decide whether voice plays a part in recognition as well as the appearance but this may be so. The personal likes and dislikes of the members of a colony can be very striking. For example in 1954 there were four pairs, K, L, M and N, who resorted regularly to four neighbouring ledges. Of these pairs L and M later bred successfully and gave the impression of being fully mature, in contrast to the other two pairs whose courtship and nesting ~~were~~ were more incomplete. Of the pair N, who were in any case only weakly bonded to one another, the male, Nestor, showed a strong attraction for the female of pair L, Lottie. Whenever Lottie's mate, Leander, left her, for example to bathe, Nestor would fly from his ledge and even leave his own female to visit her. The female would not tolerate him and as she was not able to drive him off she invariably left as Nestor approached. Leander quickly learnt that this would happen and as he flew out he would repeatedly peer over his shoulder. If he saw Nestor leave ledge N he would wheel round and return to drive off the usurper. Sometimes Nestor would return to the colony after being away for an interval and find Lottie alone on her ledge and fly to her. As usual she left and he would then start advertising vigorously on her ledge. There were several unmated females who hung about the cliff and these would fall over one another trying to get to him but he would peck each away. Lottie, whom he seemed to want to attract, might land elsewhere on the cliff and peer down at him but show no sign of wanting to go to him. His own female, Nellie, also showed no sign of wanting to visit him but was more interested in the male of pair M, though the latter would not tolerate her for more than a few seconds before pecking her away. Thus the arrival or departure of a particular individual might start a

sort of general post between the ledges. On successive mornings one could observe again and again the same pattern of changes, which became modified as new birds appeared in the circle of habituees or old ones disappeared. Often it was difficult to decide whether the interest of an intruder was really in the ledge or in a mate, and indeed both occurred, but after a time some critical situation often arose so that one could decide.

The study of the relationships of the individuals also threw light on the means by which they recognised one another. Sometimes the birds made mistake which showed that they did not use the same characters to recognise their acquaintances as I did. I saw this for example in the relation of Nestor and the L pair. During the period of day when the birds were usually at the colony the female spent most of her time at the nest while the male, Leander, frequently set off on trips to collect nest material. But if Nestor were in the colony at the time he would at once interfere and leave his ledge to circle and land by Lottie. Occasionally however it was Lottie who left the ledge, to go and feed or bathe. As she flew out I could often recognise her clearly ~~xx~~ by the conspicuous aluminium ring on one leg which was plainly visible in flight both to me and ~~xx~~ Nestor. No other bird in the colony had such a ring. But Nestor mistook the departing bird for the male and at once set out to try and land on the ledge by the defenceless female, as he thought. He was made rudely aware of his error and had to change direction at the last moment to avoid being violently attacked by the enraged Leander.

Attempted copulations were first seen in the middle of March and from that date mountings became commoner up to the time the eggs were laid. In most species the role of the male bird in copulation is to mount the female but in some, including the shag, reversed copulations occur in which the female mounts the male. Not only the act of mounting but the preliminary behaviour as well is reversed and the female may even attempt cloacal contact from above. It is difficult to be sure whether this is ever achieved. Certainly it is less common than in mountings with the male on top. The reason that shags (and cormorants) should have reverse copulations is still mysterious but certain consistencies are beginning to appear which may ultimately suggest a solution.

I tried to find out how the occurrence of copulations varied with time of day. A watch of three 3-hour periods or longer was kept on 2, 9 and 23 April 1954 from first light to 9a.m., 11a.m.-2p.m. and from 4p.m. till dark. The comings and goings of the individuals was noted and also the occurrence of mountings. These data have not been fully worked out yet but certain features are already clear. The frequency of mountings should obviously be related to the length of time the pair is together at the nest rather than the complete period the colony was under observation. Calculated on this basis the following

table expresses the mean number of minutes between copulations in the different watches.

| | a.m. | noon | p.m. | Mean for day |
|----------|-------|-------|-------|--------------|
| 2 April | 27 | 38 | 32 | 37 |
| 9 April | 31 | 38-42 | 60-64 | 40-41 |
| 23 April | 23-25 | 41-44 | 33-35 | 29-31 |

Thus it seems that the frequency of copulation is greater earlier in the day than later and that this effect is most marked early in the season. The above table is based on all the pairs under observation at the colony. When the individual pairs are considered separately one finds that some pairs show the influence of time of day while others do not. The next tables show the mean interval between copulations for pairs L and M, the two which later succeeded in rearing young.

| | | a.m. | noon | p.m. | Mean for day |
|--------|----------|-------|-------|-------|--------------|
| Pair L | 2 April | 17 | 31 | > 84 | 30 |
| | 9 April | 20 | 25-28 | 40 | 26 |
| | 23 April | 15-17 | 35-39 | 17-21 | 18-21 |
| Pair M | 2 April | 51 | 43 | 40 | 44 |
| | 9 April | 40 | 64-68 | 51-59 | 39-43 |
| | 23 April | 35 | 54 | 55-45 | 37-41 |

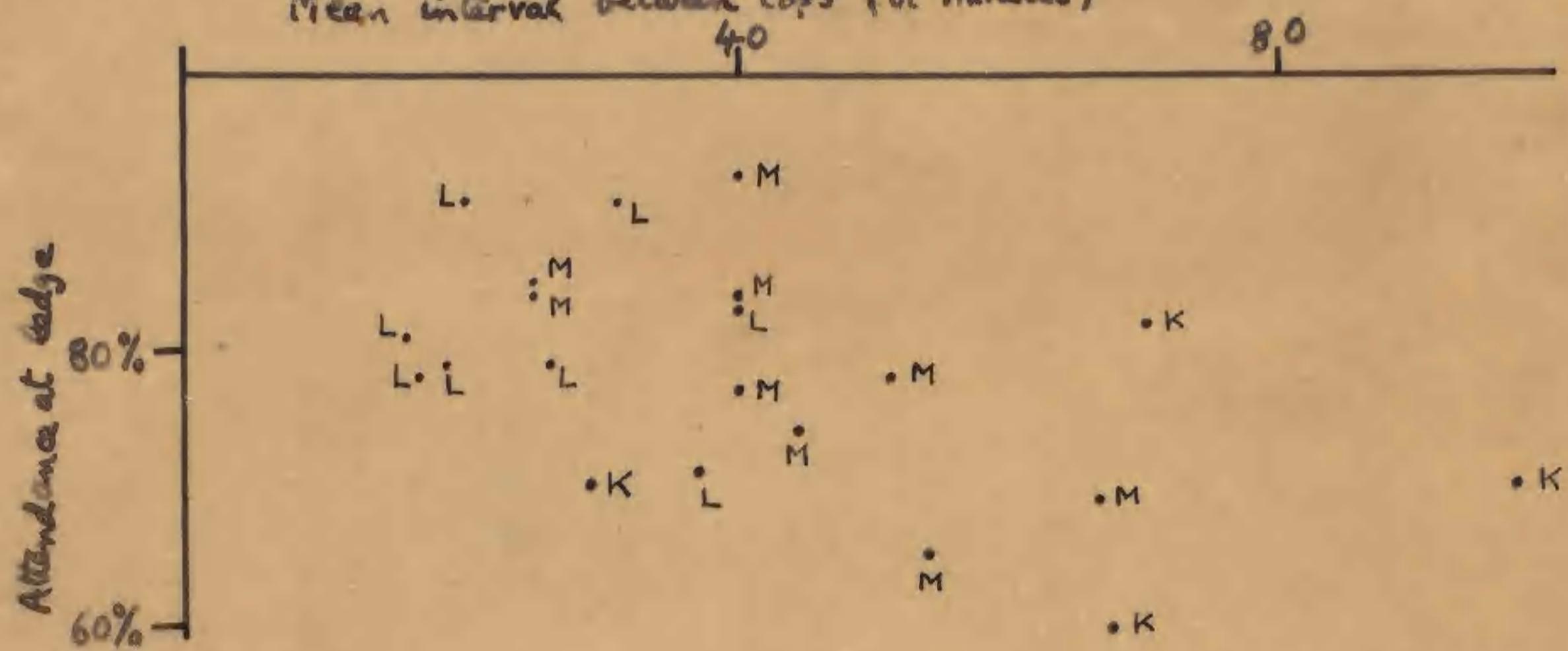
relative

A preliminary hypothesis was that the frequency of copulation (or the interval between successive ones) was a measure of sexual motivation. One could then test whether it was sexual motivation which was responsible for attracting the birds to their ledges at certain times of day. One obvious difficulty is of course that my measure of sexual motivation is really a Highest Common Factor of the sexual motivation of the pair. But in the same way one may try and express the attractiveness of the ledge for the pair by the percent of time they each spend at it. For example if the male spends two hours and the female two and a half out of a watch of three hours the percentage for the pair is

$$100 \times \frac{2 + 2\frac{1}{2}}{2 \times 3} = 75\%$$

If there were any correlation between attendance and sexual motivation we might expect to see it when the "percentage attendance" was plotted against "interval between copulations". The figure below shows the result of this plot. There appears to be a slight indication of a correlation but statistical tests show that although it goes in the right direction it might have arisen by chance.

Mean interval between cop^s (in minutes)



Furthermore if the contributions of the individual pairs are examined there is no evidence that the pair which copulated more frequently spent appreciably longer at the nest than the pair which copulated less. The conclusion must be drawn that the figures fail to show that the tendency to occupy the nest ledge fluctuates with the occurrence of sexual behaviour.

Just / The collecting of nest material is mainly the concern of the male. The first trip was seen in 1954 on 20 March. As the collecting trips become more regular one member of the pair, normally the female, ~~usually~~ stays at the nest while the other is away. The occasional lapses show that the ~~reason~~ for this is to prevent robbery of nest material. A male standing alone on his nest may show no sign of wanting to collect nest material until his mate returns, when he may at once leave and bring in load after load, only stopping if his mate once more leaves the nest. In 1954 one of the pairs, who seemed to be breeding for the first time, included a female who usually flew after her mate whenever he left the nest. His collecting bouts were therefore very short because the female flew off after him and whatever material was accumulated was robbed by a neighbour as soon as they left.

Nest material is collected mainly by diving. It consists largely of seaweed but, like the cormorants from the Megstone, tufts of dried seaweed and even campion and grass were occasionally collected from the beach on the Wideopens. Excursions to the Wideopens from the west-facing cliffs of the Farne demonstrated that the shags possessed quite a good sense of the geography of the island, for they might fly off round the north end of the island (they rarely flew over the island itself) and return round the southern side. This feat is probably not such an easy one for an animal as we might think.

Although a great many objects were seen to be brought to the nests at one time or another (including pieces of board, string, feathers and even wire netting) by far the greatest part of the nest material consisted of seaweed. Strands of *Laminaria* were much used and so were branched fucoids. Both types might be collected in one bout during which the bird visited one particular area of sea but they did not seem to be collected at random. For example a bird might make five trips in succession, each time bringing in stalks of *Laminaria*, and then three more bringing fucoids, followed by another series of *Laminaria*. It seemed that this tendency to stick to one type of material for several trips might be due to the fact that the bird was making several successive visits to rather small regions of the sea-floor where, perhaps, only one type or the other was available. However this tendency for a run on one type of material was observed even when the collecting area changed considerably. Only by observing many trips and noting as far as possible not only what type of material was collected but also the area where the bird dived could it be shown (1) that there really were runs on one type of material for a number of trips and (2) that changes in the material brought did not coincide with changes in the diving area. When both these points were established beyond the possibility of their occurring by chance it could be concluded that the birds seemed definitely to be choosing one type of material on a number of trips and then switching over to another type. The sight of either type of nest material on the sea-floor may not be sufficient for a nest collecting shag to gather it as he swims about searching. Rather he shows a preference for one type of the other which lasts for several trips. There is evidence that a "searching image" may be of importance in the feeding behaviour of tits and jays, when several different types of food are available. The more general concept of stimulus expectation seems to be more and more in use in theories of behaviour.

To speak of a searching image is of course only a convenient way of describing what is observed. It cannot suggest the reason for the behaviour. There was no evidence that I could see that the two types of material were used in different parts of the nests (contrast the kittiwake). Indeed the fucoids seemed altogether better for when they dried the tangled strands formed a three-dimensional mesh which made the whole nest more compact. On the other hand the *Laminaria* stalks and leaves never interlocked so well and often slipped off the nest before they had time to dry. Thus although I failed to understand the use of the two types of material the collecting behaviour could be used to throw light on another problem, namely the way in which the shags search for nest material.

The bringing of material to the ledge is only the first part of nest building. The main growth of the nest is due to the mere accumulation of nest material where it is dropped but there is a very characteristic movement which certainly

helps to interlock the material. The shag grasps the end of a piece and inserts it into the body of the nest with a typical quivering movement lasting a second or two. When the male brings a piece of material both he and his mate usually grasp it and make this "nest-quivering" movement with the fragment held high in the air. After holding it for a few seconds one or both may lose interest and let it fall or one of them may place it with a nest quivering movement on the nest. This nest quivering is of interest because it is used as a displacement activity as will be discussed in detail later.

The early nest collecting trips are few and scattered but the bouts become longer and longer and more and more frequent. In one of the colonies the pair L, where the female was molested whenever the male left the nest, was very slow in building a nest. The reason was clearly that the male could never make a series of trips because the other male, Nestor, would take possession of the ledge and have to be driven off. Later in the season Nestor spent less and less time in the colony and only then did the nest of pair L start to grow. As a result of this delay their eggs were laid 8 days later than an undisturbed pair, although pair L had been, if anything, earlier in their first signs of breeding behaviour.

Nest building and copulation continue until after the eggs have been laid. Then copulation rapidly dies down but nest material is brought right through the incubation period.

Two or three eggs are laid, probably at an interval of three days. Both sexes incubate but, at any rate in the early days, in different proportions. Of 388 observations at intervals of not less than two minutes at one nest, 23% showed the male to be incubating and 77% the female. All these observations were in the weeks after the first egg was laid.

During incubation the brooding bird sits quietly but from time to time rises and turns the eggs. Before rising it usually performs some nest quivering movements. The causes of this are considered later. Birds which are brooding are often subject to the heat of the sun and pant in consequence, showing a rapid fanning of the throat with bill slightly open. This panting frequently alternates with a stretching movement of the lower mandible and with another curious posture which otherwise occurs only during the preparations to regurgitate a pellet. Both the mandible stretching and the other posture may be displacement activities but it will be difficult to prove this.

The arrival of the terns cut short a further study of the reproductive behaviour of the shags. In particular the development of the young is a major gap in my observations. This will be of special interest because of the early appearance of many of the "courtship" actions which have been reported in the cormorant. If these postures result from a conflict between attack and

escape without any sexual influence their precocious appearance if less surprising. This study of the young will certainly not be made in the coming season but I would very much like to make it at some later date.

2. A more detailed discussion of pair formation.

For the reasons given much time was devoted to watching the courtship of the shags. The advertising display of an unpaired male was provoked by females (and occasionally by males until they declared their identity by their reaction to the display). One might say more accurately that those shags release the display which either behave like females, i.e. they approach the displaying bird without any of the aggressive signs of a hostile male, or else ~~were~~^{are} sexually indeterminate for the moment. For example an shag flying past the cliffs might release the display, or one flying towards the cliff where the displaying male was, though either might be a male. But as soon as the displayed-at bird showed by his behaviour that he was also a male the advertising display stopped at once and was replaced by a purely hostile form.

The advertising of the male begins with Darting. From his normal upright posture he sinks down so that his body is almost horizontal, he raises his tail and crest and coils his neck. From this posture, the Forward Posture (Fig. 1), he makes a series of rapid darts, thrusting his head in the direction of the female and then withdrawing it at lightning speed. At the front of the thrust the mouth is opened widely to flash his yellow "buccal lantern" (Selous).^(E. 2) The darting resembles the hostile gesture which I have called Shake Gaping with which a brooding shag will threaten human intruders or other shags. This resemblance between shake gaping and darting is most important reflecting the underlying similarity of motivation in both display. The differences between shake gaping and darting are also significant. Firstly the neck is very quickly recoiled after darting but remains stretched out during shake gaping. Secondly the tail and crest are more erect in darting. The stretching out of the shake gaping looks like an expression of the bird's intention to bite, that is to say of his aggressiveness. Certainly shake gaping birds are more likely to attack others than darting ones. The raising of tail and crest are less clearly the expression of a particular intention than the biting is but they do occur in the role of the lower bird during copulation. The justification of using these elements in deciding on the underlying motivation of the postures is that other indications such as the behaviour which follows the posture point to the same result. Thus when the female comes up to a darting male he may do one of three things. He may attack her, he may accept her (and stop darting at other birds) or he may even allow her to mount him as if in copulation.

Fig. 1

Forward Posture



Fig. 2. Darting

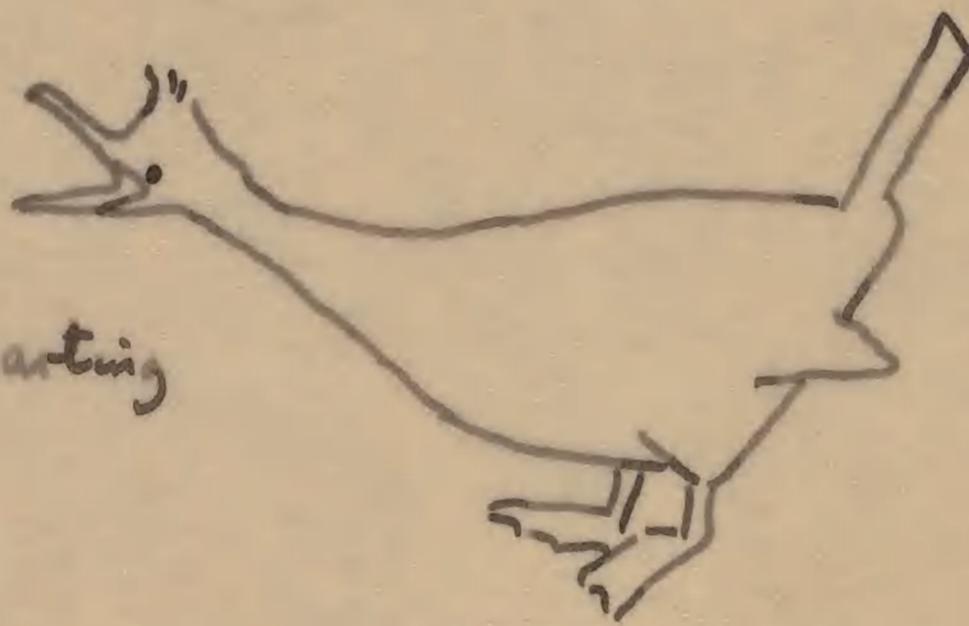


Fig. 3 Throw Back



Fig. 4 Bow

any other
regarding her?

Appendix 2.

Appendix 1.

- 12 -

But he never mounts her at once. Nor does he ever flee from her.

In the typical pair formation the male stops darting when a female shows signs of approaching him, or rather he alternates darting with another posture, the Throw Back (Fig. 3). In this the body maintains the same forward posture but the head is laid on the back with the bill pointing upwards and the whole head and neck undergo a curious axial vibration. Finally, when the female actually comes beside the male, darting and throw back stop and he performs the Bow (Fig. 4). In this the head is turned abruptly downwards so that the bill lies along the front of the neck.

The throw back and, more often, the bow may precede attacking the female although I can detect no clearly aggressive element in either posture. They never lead to the male making any attempt to escape from the female. When a male goes from darting into a throw back, the horizontal forward posture becomes even further pronounced and the tail becomes even more erect. I take this to mean that the sexual contribution to the throw back is even greater than to the darting. The bow has a close connection with the lower bird's role in copulation. A bird who wishes to solicit the mate to mount bows repeatedly. It is also used by one bird in situations where it seems to want to appease the mate, for example if the mate makes a sudden movement, always a potentially frightening stimulus to a bird. Thus, like the darting, a bird making the throw back and bow seems to be aggressive and at the same time to solicit mounting. But compared with darting the throw back and bow occur because the bird is less aggressive and more in the mood to solicit.

What is the motivation of the female as she approaches an advertising male? In the first place she is clearly very frightened of him. She adopts all the appearance of an extremely alarmed bird with sleeked feathers and long neck. She has good reason to be frightened, for as I have said the male often attacks her either when she comes up or after accepting her for a minute or two. Her extreme fear of the male makes it all the more impressive how strong must be the overriding tendency which causes her to advance towards him. One cannot say what this tendency is more precisely than that it is one to approach the male. Her main aim seems to be to get as close as possible to him and stay there. Even if he tries to peck her as she comes up she may push through his guard and take up a position beside and slightly behind him with her head held close to his and slightly behind, so that it is as difficult as possible for him to bite it. The head and neck seem to be the parts which the shags try and grasp when attacking another. ^{The Q's behavior} This is sometimes successful in preventing attack and the male's aggressiveness often dies down so that she can relax a little.

But at any renewal of his aggressiveness she once again tries to hold her head where he cannot reach it. If she is very frightened she may even point her bill away from his head, though keeping her head very close behind his. This gives the impression of trying to hide her face from him but more probably its reason is a preparation to flee.

Reason?

Mounting may
which ever did
not result in
a result?

As already mentioned the visit of a strange female to a male may actually lead to her mounting him. I am not sure yet when this happens but it may be that the female's tendency to approach the male is an expression of the sex tendency of the mounting bird. That she does it so rarely may be because she is usually too frightened. The female shows no inclination to attack the male or even ~~try~~ to threaten him, so that one supposes that her aggressiveness is not aroused.

Something has already been said of the origin of the darting posture of the male but no attempt has yet been made to explain why an unmated male should adopt the recumbent posture which in other species we associate with the female's pre-copulation posture. One would suppose that this posture would be effective in attracting an unmated female only if she showed a very strong urge to mount the male. Apart from the fact that she may (occasionally) mount him in spite of great fear, there is little to support this suggestion. Of 170 mountings noted during 1954 only 12% were mountings of the male by the female. At the moment one must leave the problem here but further light would certainly be thrown on it if the causation of reversed copulations was understood.

A comparative study of the advertising display of two other species of cormorants can be made from the published descriptions. A comparison of these species, the European Cormorant *Phalacrocorax carbo* and the Brandt Cormorant *P. penicillatus*, with the shag *P. aristotelis* is revealing. This is not the place to enter into the details but some conclusions may be mentioned. When we try and compare the different displays it is easy to recognise some postures which are similar enough for one to suppose they are "homologous", i.e. they were possessed by a common ancestor. For example all three species advertise in the forward posture with body tilted and tail raised. But other postures cannot be homologised ~~as~~ until we consider the elements separately. It is then found that the elements are combined differently in the three species. One is now left with some features in each species which are not accounted for, including the shag's bow and the slow waving backwards and forwards of the head of the cormorant. The Brandt cormorant has something intermediate, the so-called Stroke. These movements differ mainly in their speed, two, the bow and stroke being abrupt, the other rather languid. Since there are already indications in other species that alterations in rhythm are just the sorts of changes which take

place in evolution, it may well be that one can homologise the basic features of these three movements. It must not be expected that all the advertising display elements can be homologised. The European and Brandt cororants both have a very similar display called Wing-flapping and the Flutter respectively. The shag has no trace of this that I can see but has instead the darting. According to my interpretation of the postures the darting would be more aggressive than the wing flapping and flutter and therefore I could expect visiting females to be attacked more commonly in the shag than in either of the other two species. The test of the correctness of these views must always be comparison with yet other species but they already appear plausible.

3. Nest-quivering as a displacement activity.

The characteristic nest quivering movement has been described. Much nest quivering occurs in connection with the collection and depositing of nest material, that is on occasions when all the nest building activities are active. However a ~~unin-~~ shag begins nest quivering in two other situations which seem to be causally different from each other and probably also from the normal complete nest building.

If a strange shag lands close to the owner of a nest the latter will generally attack and drive off the intruder. If the intruder does not come so close the owner will probably shake gape at it a few times, perhaps alternating this with nest quivering, and then lose interest. If the intruder stays away ever further still the ~~owner~~ ^{intruder} will probably nest quiver a few times and then pay no further attention. The stimulus of an intruder can thus cause the bird to attack, ~~shake~~ gape or do nest quiver. Both attacking and make gape are aggressive expressions but one would not expect the nest quivering to be. Nevertheless it occurs in many of the situations where the tendency to attack is activated and one is forced to conclude that it can be activated by aggressiveness.

Very many activities have been described in birds and other animals which are like the nest quivering in appearing outside the normal ~~more~~ functional and causal context. Few detailed studies have been made of these so-called displacement activities and the name has certainly been attached incorrectly to some. Fortlandt in making his very thorough study of the cororant applied the name to many patterns in what was, at times, a most improper way. Indeed it was just because of the conveniences of the concept for concealing ignorance about causation that he has failed to recognise the attack and escape element in pair formation. But in spite of the dangers of its use there really does seem to be a core of truth in the idea of displacement activity and it is therefore of great importance. The only valid test for displacement activities seems to be the study of their causation. Fortlandt included the nest quivering in

his examples of displacement activities and this certainly seems correct as far as I can judge.

*Why must even if it is
extensive that
it is displac-
ment?*

The nest quivering occurs in prolonged nest building activity but it is not very easy to decide on purely observational evidence what external stimuli, if any, release it. However there are two other situations where I can show that it is likely that the releasing stimuli are of two quite different kinds. I have already described the first, how nest quivering can be released by an intruder. And I have mentioned the second more briefly, how a brooding shag nest quivers shortly before rising to turn its eggs. I have given reasons to think that the intruder arouses some degree of aggressiveness in the incubating bird. Whatever stimuli signal the time to turn the eggs, there is certainly no reason to suppose that they make the bird aggressive. At any rate the shag never shows any other sign of aggressiveness when about to turn its eggs and one must suppose that whatever makes the bird turn its eggs also makes it nest quiver. One can dispose of the possibility that it is the nest quivering itself which causes the turning. These two situations do not cover all the occasions when nest quivering occurs but they are the two when I have been best able to decide anything about the stimuli provoking the behaviour.

*Q. It too
seems a bit
muddled at
first.*

To summarise, the nest quivering is released in one instance by stimuli from an intruder which probably activate the aggressiveness of the shag, in the other instance it is released probably by some stimuli from the eggs activating the tendency to turn the eggs. There are therefore at least two causally different types of nest quivering.

4. Postural influences on displacement activities, etc.

Long hours of watching inactive shags waiting for something to happen became more interesting when I started to watch the "comfort movements", their ways of preening themselves, how they oiled their feathers, how they scratched and how they stretched and yawned and slept. This showed me many aspects of their daily life which I hadn't expected: that they rarely preen their tails, that they always use the third claw to scratch themselves and that this claw is provided with a special comb, that they hold out their wings to dry after bathing, but not as long as cormorants. But it also made me aware of something which seemed more important in the fundamental problem of why animals behave as they do.

The shags have a display movement which has an appeasement function towards potential aggressors. I have called this movement the Upward Gape. I noticed that this display was quite often followed within a second or two by another movement, a very characteristic stretching of the upper mandible. If the two

occurred at random one might still expect that occasionally they might happen in such quick succession but the frequency with which I saw it ruled out this possibility of mere chance. There was clearly some kind of causal connection between the two movements. Both movements had in common that the beak was pointed rather above the horizontal and then opened. There seemed a similar kind of causal connection between two other movements: defaecation and both wings stretch. In the first the body is tilted forwards and the tail raised; in the second both these things happen but also the neck is stretched out in a peculiar manner and both wings are raised above the back though usually not unfolded. The both-wings-stretch posture occurs in most, if not all, species of birds but the defaecation posture is more variable in form in different species. Instead of the typical defaecation posture I saw that a shag might often adopt the both-wings-stretch posture when defaecating, either at the time or a few seconds later.

In both examples given the link between the two postures must which seem to be connected was in the form of the movement. The adopting of the one posture seemed itself to serve as a stimulus for the other to follow. There was even some evidence that there was a reciprocal effect. Not only would the upward gape stimulate the upper mandible stretch but the upper mandible stretch would stimulate the upward gape. The hypothesis is that the posture of the birds, that is to say the actual tension of the muscles and their relations may influence the immediately subsequent behaviour of the bird. It may for example sometimes determine the nature of a displacement activity. Indeed the examples I have just cited might be called displacement activities. The wing-flapping in the advertising display of the cormorant has already been mentioned. No one has yet offered any suggestion at all as to its origin and before attempting to do so one must consider the movement more closely.

The wing tip is raised upwards while the carpal joint is hardly brought out of the supporting feathers. This is achieved by a rotation of the humerus. Now this rotation is a peculiar one and as far as I can see occurs in only one other situation in a cormorant's normal life: when it begins to make a both-wings-stretch. In the advertising display the male cormorant is in a conflict situation which, in a great many species, is known to result in displacement activities. I think it possible that the choice of a displacement activity may have been determined by the posture in which the bird was at the time, the forward posture. This requires one to suppose that the forward posture is older in evolution than the wing flapping but this is not contradicted by the few facts available at the moment. Once the displacement wing-stretch was likely to occur the further process by which the rhythmic raising and lowering of the wings was evolved must have been due to some kind of ritualization, a word which does little except cloak our ignorance but it would be something if the first step were accounted

for.
First night
Cormorant displacement activities etc.

The Breeding Behaviour of the Arctic Tern.

A great many words have been written about terns and it is a considerable effort merely to read this body of literature. In such matters as the longevity and tendency to return to a former breeding place a great deal is known thanks to the work of the Austins on the Common Terns in Cape Cod, Massachusetts. Nevertheless most of the studies of behaviour have been descriptive and it was hoped that a start might be made on an analysis of the causation of the behaviour in same sort of way as had been done with the gulls in the development of Dr Tinbergen's programme of studies. For this reason I spent a fragment of 1952 and the summers of 1953 and 1954 in watching the reproductive behaviour of the Arctic Tern. I made little systematic attempt to study the fishing apart from a purely descriptive one. The way in which the terns find fish is certainly interesting and it is very impressive how quickly a group of diving birds attracts others. One can also make out certain regularities in the places where they choose to fish. Near the island they select the zone around the patches of upwelling water where the tides run fast over some irregularity. I collected samples of a few preys and over a period of two weeks when the young were being fed I counted the proportion of sand eels and other preys carried by parents. This showed that the proportion of sand eels, by far the commonest prey, varied ^{on different days} between 58 and 92%. Such a difference must have reflected a real difference in the prey caught. The next commonest prey at this time of year was what was probably one of the herring family. One such fish which I was able to examine was a young Herring. It appears possible to me that not only is the forked tail of terns a specialisation for fishing but that here might also be a reason why the forkiness of the tail varies so much from species to species. If one compares the fishing of Sandwich and Arctic terns it seems that the larger birds get their prey more frequently by diving. The Arctics usually feed by merely swooping to the water surface and picking something off, often without immersing themselves. Perhaps (and as yet I can say no more) it is the half-folded wings which exercise the main control during the steep dive while in the shallow swoop the tail plays a greater part. One could certainly find out whether it is true that the Sandwich really dives more than the Arctics and one might even find differences between Arctic and Roseate. The Roseates around the Inner Farne were rarely seen fishing by me. Their usual method of getting food seems to be to chase other terns and snatch the fish from them. They certainly have amazingly quick powers of turning which would be facilitated by their long tails. Although they are able to fish like the other terns it is probably no coincidence that with such a swift flight and powers of turning they are adept at robbing fish. Arctic and Common also try to but rarely succeed.

Before the terns came I had been watching the shags and the change was a very abrupt one which it took me a little time to adapt to. To watch what a tern does requires far more concentration. Not only are all its movements far quicker but so are its changes of "mood". At one moment it is standing on its territory calling at flying birds, the next it runs at an intruder and flies the last few feet to drive him off before hurrying back again. A female visits him but before they have been together more than a second or two a sudden panic seems to alarm the whole colony and both birds sweep out with all their neighbours silent except for a few alarm calls. As they wheel over the Kettle the earlier calling and excitement starts again and the birds return to their territories or to the preening places on the water's edge.

These curious panic-like performances are a frequent feature of the life of the colony, particularly during the early days at the colony. Indeed one sees them taking place even before the birds alight for the first time in the year on their colony area. They may take place as a reaction to some genuine scare, such as a person walking about or they may be precipitated by a single bird whose sudden silent flight out from the colony towards the sea excites others with a common fear, who in their turn alarm their neighbours. In this way the whole colony, or a part of it, may fly out. These panics become less common as the birds become more familiar with the colony area and its normal equipment of human beings and finally the birds become quite blasé about even large crowds of visitors. In the same way at the end of the season the panics again become commoner before the terns finally leave the island.

Panics of this kind seem to occur in many or all colony nesting birds. They are a familiar ~~mark~~ feature of a Sand Martin colony. There is no doubt that the birds are frightened as they fly away from the colony. A natural experiment demonstrates that the terns during these panics avoid not only their colony but land of any kind. At low water springs the Inner Farne is separated from the Wideopens by a narrow channel only. When the terns panic on the Inner Farne at any other time, they fly away from the Farne and towards the Wideopens. But at low water springs they seem to be deflected by the sight of the Wideopens close in front of them and fly towards the Knox's Reef. The panicing birds not only fly away from land but they tend to bunch into a flock. The flying away from land presumably protects them from ground predators; the bunching is supposed to be a defence against an aerial predator but it is difficult to confirm this. Both types of behaviour take place even though there is no sign of the predator against whom the activities seem to be a defence. There seems no evidence that the behaviour is anything in the nature of a social display as has been suggested. The panicing birds show no behaviour which does not seem to be the outcome of fear. The name of panic is suggested at once by the apparently

spontaneous nature of these alarms. However one may by chance notice one of the first birds to become alarmed. On these occasions it seems that it is the behaviour of the frightened bird and the calls he utters which infect his neighbours, who in turn spread the panic to the rest of the colony. There is indeed no need to suppose some telepathic influence simultaneously affecting the behaviour of many birds at once.

The earliest Arctic terns seem to arrive at Budle Bay towards the end of April. At first for a few days we did not see than around the islands but ones and twos soon appeared and very quickly the birds could be seen flying from the west towards Knox's Reef and settling there, especially in the morning. Later in the day the flock there seemed to become smaller and odd birds and little groups would be seen on their way back to Budle Bay. These morning visits would involve quite a lot of aerial display but the birds rarely came over the colony area at first. In 1954 the ~~xxxxxx~~ came rather late and the first bird, a Common tern as it happened, was seen to land on the colony area two days after the first Arctic/Common had been seen in the Kettle. The pairs become suddenly much more frequent as the first birds begin to touch down but only a few land before all gradually move away out over the Kettle again and the day's activity at the colony is over. These morning visits become longer and longer, beginning earlier and ending later. There is no trace of any evening visit. Although the visits become longer the terns do not roost on the island until shortly before the eggs are laid. ²

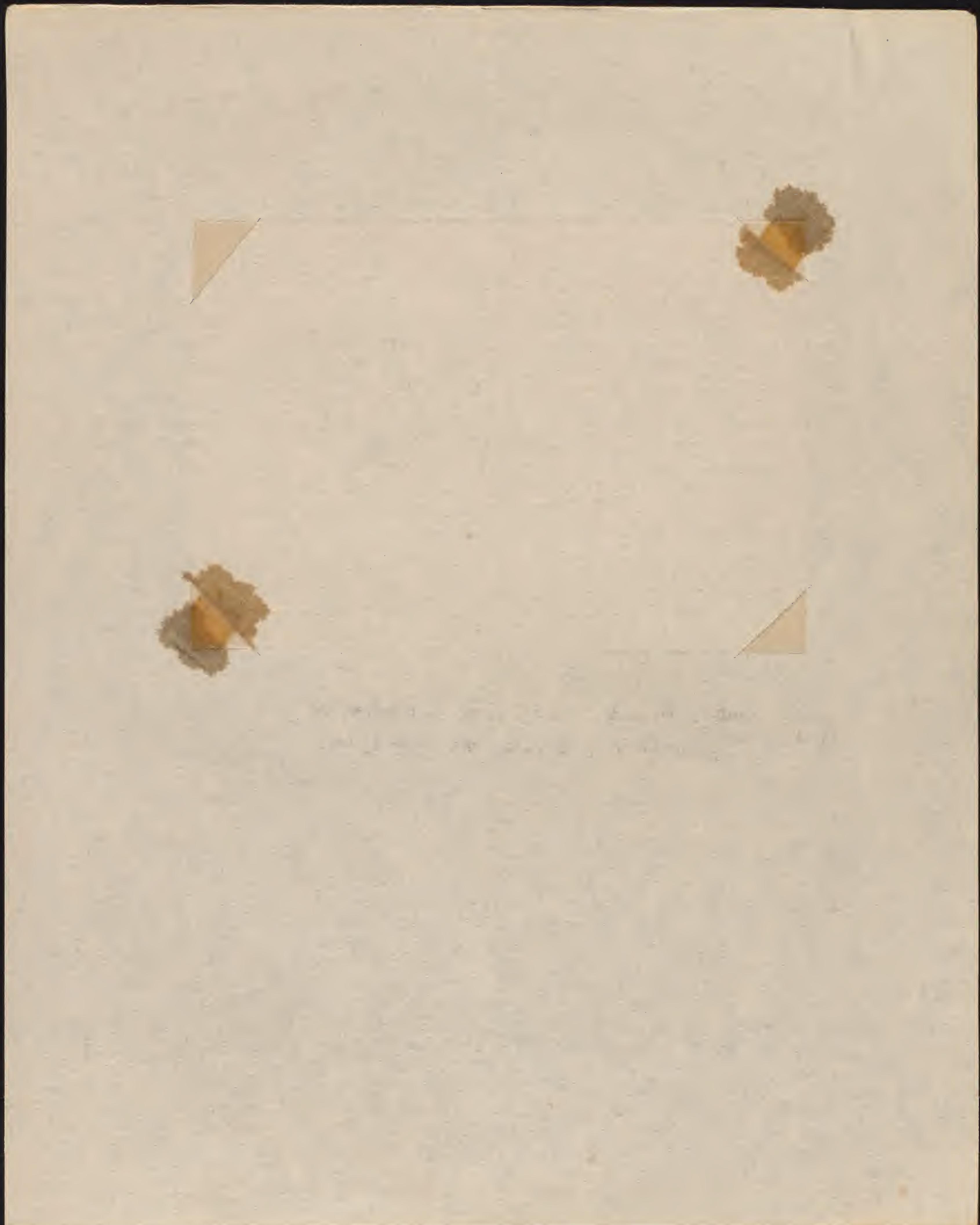
Let us turn now to the behaviour of the individuals. Because of the difficulty in following individuals in flight for more than a few minutes at a time, it is not sure how long two birds which perform the aerial display together remain in company. Probably they don't because the first birds to land on the ground are visited by others (presumed females) who don't seem to stay with them but may visit several of the "males" in turn. For these reasons I think it is likely that the pairs do not remain together in winter. Pairs are sometimes reported in company on migration but they may only be temporary partners. In one instance I knew two males who were colour ringed from an earlier year. Each had bred the year before with a mate whom I had also colour ringed. The names of the two pairs were William & Mary and Dick & Dot. On 15 May 1954 I saw William, Dick and Dot for the first time that year (and I think it likely that they didn't visit the colony before). Dot showed no immediate attraction for her old mate, Dick. On the contrary she made an aerial display with William of a type which I suppose to be an early step in pair formation. However later in the day she stayed near Dick and did the same aerial display with him. In the end she rejected both males and mated with quite a different one some yards away. Late in the season Dick had still failed to get a mate but again and again would bring a fish which he would carry about for several minutes. This is a part

of the behaviour of unmated males seeking a female. Again and again his one-time mate, Dot, would fly to him, beg the fish and take it to feed her own young. This does not constitute any act of recognition between the two birds though the male may have recognised the female. He behaved towards her as he would to any female he was trying to pair with. On the other hand her treatment of him was quite unlike that of a female towards her mate but was the way a female feeding chicks might react to any bird with a fish. The fact that the terns tend to return to about the same area of the colony where they bred or tried to breed the previous year will of course tend to bring old pairs together again and indeed I had several pairs, including William and Mary, who bred together in successive seasons. It is difficult to decide whether there is any preference at all for the mate of the previous year (as was found in the kittiwake) but it would seem likely because the nest site of the previous year cannot be located very accurately on the sand. During the winter the height of the beach shifts and changes occur in the landmarks on the sand. The fact that pairs rejoin one another inspite of this suggests that they must retain some memory of the individual appearance of the old mate or of its call. This is not surprising as they certainly learn the appearance and voice of the mate during the season.

The behaviour of males before they are paired consists of resorting again and again to a small area of ground, perhaps only a few feet in diameter which they use as their head-quarters in their efforts to attract females. Although the birds may return regularly to quite a limited area they do not spend their time there continuously. For example Dick who failed throughout 1954 to get a female nevertheless performed his advertisement displays (to be described later) only in a small part of the area where I made my day to day watches. I could not exclude of course that he did not display anywhere else in the colony or outside it, but the fact that he did not display in other parts of the study-area suggests that his sphere of influence may have been quite small. He displayed there from 15 May until mid-August though often I saw no sign of him for several days. Some birds were clearly not restricted to a single display area throughout the season and a few even resorted to two areas alternately though both were quite small, a few yards in diameter. Thus I believe that the males who are seeking to attract females display in particular spots which they choose in or around the nesting area of the colony. But they spend no more than a small percentage of their time actually in these areas. This was one of the difficulties in watching the behaviour of unpaired birds to discover how they received females. One might watch an area where one morning's observations had shown that a certain male spent his time. The next day he might be completely absent during a watch of 5 or 6 hours and the following day he might appear again for only half an hour or so. On the whole it seems that the mornings are the most likely time for birds to visit their territories but even then there seem to be gaps



Fig. 1
Greeting. The male in front is in the Bent Posture, the female behind is the Stretch. Note tilting by both.



on some days. What do the birds do the rest of the time ? Certainly they must spend much of it fishing which cannot be done in the territory. They also tend to alternate time on their territory with visits to the flocks which sit about at the water's edge close to the colony. The birds at these preening places spend their time resting, sleeping and preening, all of which they can and do on their territories. They ~~xxxx~~ show a slight tendency to display there too but such displaying birds seem to be already paired. It is therefore difficult to know how and where a particular individual is spending his time and it becomes impossible to describe all his behaviour towards potential mates. After the liaison between a pair is just beginning the two may fly off together and stay away for hours. This can be perfectly maddening. Although the birds may return again and again to one (and sometimes more) small areas, I have as yet said nothing about the defence of these areas. Some males defend their areas fairly thoroughly, driving off trespassing males and perhaps even potential mates. But the majority seem to behave to most intruders as if they were females and to try and court them. This may change into attack if the other bird is hostile but it generally has the same end result as threat and causes the intruders to fly up.

The postures with which a male responds to the visit of a female have been frequently described by earlier observers. There are two of them the Bent and the Stretch. The Bent is shown in Fig. 1 and is characterised by the pointing down of the beak, the stretching forward of the neck, the drooping of the carpal joints and the raiding of the tail. It is accompanied by a special call. The stretch, Fig. 1, has the same drooping of the wings and raising of the tail, but less strongly, while the neck and bill stretch upwards at an angle varying from the horizontal to the vertical. These brief descriptions will suffice for the moment. The alighting bird usually assumes the stretch as it lands, while the male on the ground makes first the bent. He may then adopt the stretch also or he may go and scrape or first one and then the other. In the scraping the breast is lowered to the ground and the feet scratch backwards to throw out sand. In this way the use of breast and feet hollow out a scrape in the sand similar to the one in which the eggs are later laid. The postures of the male and female which usually precede scraping have been called a greeting ceremony and I have used this useful name. During the scraping which follows greeting the female tends to be attracted to the spot where the male is performing and may even perform there herself. This may be important in acquainting the female with the male's territory and the most important focus in it, the nesting scrape.

Not only does the male adopt the bent posture as the female alights but he adopts it as a reaction to flying birds and it often seems to attract females. The landing of the female then causes the posture to be more exaggerated.

But the males have more than one way of attracting a female into their vicinity. Such birds, especially if they have not been visited much by females, may perform an advertising flight. This is made to and fro over the colony area but sometimes takes a male farther afield. In this flight he makes himself thoroughly conspicuous flying rather slowly and calling frequently. He is inclined to approach other flying birds as well as birds on the ground and he seems to try and induce the other bird to fly up and join with him in performing a ceremony I have called the Pass. In this one bird flies past and over the other and takes up a position in front of it. As it passes, the overtaking bird assumes a posture which seems to be the same as the ground stretch posture, so far as this is compatible with flight, and this posture is maintained as he flies in front of the other. The bird who is overtaken adopts what seems to be the aerial equivalent of the bent. An unmated male making the advertising flight tends to adopt the aerial bent posture at the approach of or flying near of another bird and he is inclined to fly towards the other bird. This seems to induce the other to perform the stretch role in the pass. The flying-over bird not only has to adopt the stretch posture but he also has to follow the manoeuvres of the bent bird. That this is done from a position in front of the bird to be followed seems rather surprising but there is no doubt that the terns are well able to do this. Indeed if the manoeuvres of the bent bird are so sharp that the stretch bird falls out of position and comes behind the other he again overtakes and comes to fly in front.

In terms of its purpose the ceremony of the pass seems to test how far the stretch bird is content to follow the lead of the other. This is supported by the later behaviour of the bent bird who, when he has been successful in finding a female who will stretch over him and follow his movements, will lead her to land on his territory. As he lands and she comes down beside him both enact the normal greeting on the ground which was described above.

The behaviour with which a male on the ground attracts and greets a female has certain important features in common with the advertising display flight. Neither occurs in very aggressive males. Both occur or become fully expressed as a reaction to other birds nearby, especially when those birds show some inclination to approach the male in the stretch posture but not when the other shows hostility. Finally the purpose of both displays seems to be to focus the interest of the female - either to draw her attention from the colony area as a whole to a particular territory or from the territory as a whole to the male's scrape. The latter is important because the scrape or scrapes which he uses are not necessarily in the middle of the area which he defends. It would presumably lead to the disadvantages of prolonged fighting if the female laid in the scrape of a neighbour

for the pair would then have to conquer the spot which might have been used for laying in the absence of the owner.

Why should the terns need an advertising display flight as well as a ground display to attract females? Though they do nest (mainly) in the open the territories are relatively small so that the female, flying around, would simultaneously be within sight and sound of a number of males who are seeking to attract her. Males who developed an aerial display would not only be able to press their attentions more assiduously but they would be able to attract females from a much greater distance than if they could only attract females by their postures and calls on the ground. One need not emphasise that a flying bird is more conspicuous than one on the ground, if only by reason of the greater movement. Such advantages would accrue to most species of birds and indeed in many different groups a ~~courtship~~ flight has been evolved to advertise the unmated males. The gulls have an aerial threat display and this may have given rise to the aerial courtship of the terns. The lack of aerial courtship in the gulls may be due in part to ~~xxxxxx~~ their greater reluctance to take flight than the smaller terns.

After the pair is firmly established the male brings fish which are fed to the female. This is fore-shadowed in the earlier relations of the pair when the male often carries a fish. Unmated males who are visited by several females may carry a fish and even in the aerial display before the birds have visited a territory and, it is repeated, on migration a fish may be held. One can see that females are attracted more readily to males who carry fish than to males who don't. This might just be because the female is always hungry but sometimes it is more than that because after getting the fish she holds it without swallowing. The reaction of a female to a male with a fish is evidently not merely a result of her hunger but of something connected with her getting a mate.

A male may spend some time on his territory reacting to flying birds and others and then fly off and return with a fish. At once a striking difference comes over his behaviour which, as soon as the fish is lost or swallowed, reverts to its earlier mode. When he has a fish he spends far more time in the aerial advertisement flight than in the ground advertisement. He also shows a greater inclination to visit birds who by their posture look like females. The actual displays themselves, as opposed to their frequency and their effect on females, do not seem to change. He may succeed in leading a female to his territory but for the female the possession, though often not the swallowing, of the fish seems to be her aim. She tries to get the fish ~~xxxxx~~ by fair means (a special begging behaviour) or by foul (snatching it). Consequently a male who gets a fish may not keep it long but may lose it to one of the females who visit him. Or he may swallow it himself. In either case at once he changes

back to the ground advertisement of earlier.

Another fact is apparent from watching such males. Not only does the possession of a fish cause the male to be visited more often but fish-less males visited by a female are stimulated to try and get a fish.

The web of behaviour is further complicated because males are not content to catch fish for themselves. They also try to get them from males who have fish. They use, as far as I can see, exactly the same postures and behaviour in trying to get the fish as does the female. But as soon as they have it they at once leave the male and return to their own territories to sport their trophy and attract females and perhaps, with poetic justice, other covetous males.

The visit of a female may lead to greeting or, if there is a fish, to its presentation to the female. Either event is typically followed by a new type of aerial display, the High Flight. This shares certain features with the advertising flight described before, but seems to be qualitatively different. Unlike the advertising flight the high flight is a dual performance from the beginning ~~and~~ ^{and} both birds fly up and ascend in small circles as if they were following one another up the same spiral stair-case. This ascent has special features including the type of flight and the calls uttered. It lasts up to several minutes and then begins a fast glide, steep at first becoming shallower as the birds approach sea-level. During the glide a number of passes occur, as in the advertising flight, but with a special difference that the male, who initiates the glide and behaves as if he were pursuing, is the stretch bird in the first few passes and later in the bent role. The female has the other role. As in the previously described passes the stretch bird, whether male or female, follows the manœuvres of the other while remaining in front of it. It is significant that in spite of the male's stretch role in the first few passes, at the end he has regained the role of director, one cannot say leader, of the flight. It is also clear that he is much more eager to regain it than is the female to relinquish it. Once again it seems that the behaviour is aimed to test whether the female will accept the male's ascendancy in determining such matters as where they will fly. If the female will not adopt the stretch role the male separates from her and the ~~xxxxxxxxxxxxxx~~ formation of the pair breaks off.

It is fairly easy to understand in an anthropomorphic sense the function of the various ceremonies which take place between the pair. One can translate the anthropomorphic language into something more scientifically respectable but only at the loss of conciseness. I shall not attempt to do so here but merely point out that one need not presume any understanding by the bird of the actions which it performs. To

understand the more immediate reason why a bird should act as it does it is helpful to think of the bird as being all the time under the influence of one or more of a number of tendencies or drives. When a bird stops bathing and starts to preen one can say that there has been a change in the predominating tendency from bathing to preening. Most of the time a bird seems to do one thing at a time but the fact that towards the end of bathing some birds begin to intersperse a few preening movements with their bathing shows that the new tendency can begin to express itself before the whole pattern of behaviour has switched over. This idea of fluctuating tendencies has been specially valuable in the study of reproductive behaviour in all species where it has been attempted. In the formation of the pair the mates of many species react to one another by attempts to copulate, to flee or to attack. One can, with practice, recognise all three kinds of attempts and one sees that when the behaviour of the pair does not lead directly to one of the three there are indications that one or two or all three tendencies are active. Indeed by using these indications one can go far to examine what underlies the indecisive-looking actions which comprise what we call courtship. It is useful therefore to see how far it is possible to explain the various courtship and threat displays in terms of these three tendencies.

In my study of the Arctic tern I am still very much in the descriptive stage in understanding the pair formation. Something of the function is already apparent but I can only guess at the causation. Once the pair bond is well established the motivation underlying the later behaviour is rather easier to understand. The male starts to feed the female regularly and ceases to show the hesitation of the early days. As he approaches with food she is much more ready to adopt the typical Hunched Posture with neck withdrawn of a food-begging female (or chick) and less likely to make the stretch as she did in the early days. The female now spends more time than before sitting about in the territory and she food-begs very strongly as the male comes in with a fish. She distinguishes him from other males with fish and seems first to recognise him when he is several yards away.

From the time when frequent feeding of the female begins, and probably often from a much earlier stage in pair formation, the male shows an inclination to try and mount the female. At first she is usually too frightened to allow such close contact but I have seen a male succeed in climbing on at what seemed to be the beginning of the pair's acquaintance though I could never be sure how much they might have been together away from the territory. In his pre-copulatory behaviour the male first starts to make a sort of parade in circles round and round the female and she at first usually tries to move away from him. If a movement of hers frightens him he will move farther from her but continue circling, while as he prepares to mount he gets closer and closer. As mounting becomes more imminent still his circling changes to walking to and fro

in a semicircle around her head end, turning each time he gets on her flank. This turning I interpret as a sexual expression of preparing to mount. At first the turning doesn't lead to mounting but the continued presence of the female in her typical pre-copulatory posture seems to provoke him sexually more and more until it finally overcomes the last obstacle and after turning on her flank for the last time he half-flies on to her back. Sometimes the male will not mount however much the female solicits him and at other times it is the other way round. Sometimes one can recognise that the reason that one of the partners does not proceed with the appropriate copulation behaviour is because it experiences too great a tendency to attack or escape. Indeed one may see an actual attack on or avoidance of the mate. As the male comes closer and closer to mounting his neck becomes longer and longer, as in many other birds. This seems to be an intention movement of mounting the female. But he also sometimes shows a number of bowing movements of his head in which the beak, which is normally carried horizontal, is pointed downwards and then returned to the horizontal. I tried to discover what this bowing was due to. The movement slightly resembled one of the commonest threat movements with which terns react to neighbours and sometimes to their mates. But the movement came closely before actual mounting at a time when I did not expect the male to be aggressive. Another possibility was that it might be an alternation of the intention movement of mounting with the posture in which the male stands on the back of the female after mounting. In this he looks downwards at her head as he also does during the act of copulation itself. However it turned out that it was more likely the aggressive movement, because when I looked at the pre-copulation behaviour of other species most of them had the looking down of the mounted male and might be expected to show the alternation of this with the pre-copulatory neck stretching, but none of them had the bowing before mounting except the common tern, which was also the only one to have aggressive bowing. This sort of evidence is one type which is used. Another type is necessary but may be less easy to collect. The pre-cop behaviour of a male occasionally leads it to attack a female. If the pre-cop bowing were aggressive one would expect it to be commoner in those pre-cop sequences which ended in attacks than in those which didn't. I don't yet have enough sequences recorded to decide.

This rough survey of the behaviour which leads from pair formation to copulation is incomplete without any mention of the manner in which terns treat their opponents. Territorial encounters may lead to attacks, fights, or fleeing, or more usually ~~or~~^{as} break off in a less decisive fashion after some posturing by the opponents. The posturing is less indecisive than one might expect at first and the opponents seem to react to it as comprehendingly as if the other actually made an attack on them. Posturing birds in territorial encounters may move towards an opponent or away from him or the posturing

may be precipitated into actual attack or fleeing. Apart from the tendencies to attack and escape one sees little sign of other tendencies common to all the situations where the postures occur so that one tries ^{now} for these two conflicting tendencies alone can account for the observed behaviour. In the first place one sees that a posturing bird may walk a few steps towards, then a few steps away from its opponent so that it seems the predominating tendency can change quickly from approach to escape. But much of the time the bird is content to stand still albeit with signs of excitement so that one might expect that aggressiveness and fear are active simultaneously. From a study of other species it seems possible that the particular posture used depends on the ^{actual} strength of these two tendencies. Let us consider the terns' postures in detail.

There are three postures which I call the Crouch, Bowing and the Slant. None of them seems to have been described before. Any of them may be followed by attack or escape so that one could at best expect to find quantitative differences between them. In the crouch, the rarest of the three, the whole body is tilted forwards, the beak points downwards and the neck is withdrawn. It becomes ~~more~~ common only after the eggs are laid when neighbours meet one another on their territorial boundaries. Prior to egg-laying the boundaries are more fluid because it is rare that all the neighbours of one pair are present at the same time. The crouch also occurs after the young hatch when they begin to wander outside their own territories and through those of their neighbours. The parents follow them and bitterly resist attempts by the owners of the territories to drive out their young. The crouch seems to occur only when both opponents are thoroughly aggressive and yet do not dare to attack in the face of the threatening aspect of the other. Sometimes such threatening bouts last for a couple of minutes with the birds practically motionless (an enormously long span for a tern to remain inactive) and then a slight turning away by one bird or the uttering of an alarm call may precipitate a violent attack on it.

The Slant and Bowing also repel intruders but there is far less tenseness in these situations and when they do lead to attacks ⁱⁿ the onset is less furious. For these reasons I think that these two postures each of the tendencies, to attack and to escape, ~~are~~ less strong than when the crouch occurs. It fits well with this that the orientation of the opponents is far less precisely directed towards one another in the slant and bowing than in the crouch.

In order to distinguish between the slant and the bowing I tried to find if one led to attack more frequently than the other. When the young terns are more than a week or so old, the adults leave them alone for long periods while the fetch food. In their absence it frequently happens that an intruder, adult

or chick, wanders close to the unguarded chick. When the parent returns it usually feeds the chick first and then threatens and even attacks the trespasser. The following table shows that the attack is more likely to follow the slant than the bowing.

| Led to: | | Threat posture | | It shows the number of observations in which either threat posture did or did not lead to attack. |
|---------|-----------|----------------|--------|---|
| | | Slant | Bowing | |
| | Attack | 27 | 3 | |
| | No attack | 24 | 51 | |

From this one can only conclude something about the relative balance between attack and escape, namely that the attack tendency is relatively stronger in the slant than in the bowing.

In the study of some displays it has been found possible to analyse two alternating components of a movement and identify the two postures which alternate. The bowing looks like a movement which could be studied in this way and I found that of the two postures, the upper phase of the bowing seemed to be identical with the slant. The lower one I failed to identify but it seemed significant that in it the black cap was directed towards the opponent just as occurred in the crouch. This will be discussed later. If the bowing is relatively less aggressive than the slant, as I concluded from my counts, and is in fact an alternation of the slant with some other posture, this suggests that the undiscovered posture is even less relatively aggressive than the bowing. Thus although I could not discover the actual posture in the Arctic tern one can already say something about it which may help in finding it in another species where it may still occur.

There is yet another posture which may occur in a territorial encounter, the stretch. It does not precede attacks (though I have seen this once or twice) but seems rather to be an expression of fear. For example a male may alight by accident just outside his territory in that of a neighbour who at once prepares for attack. The alighting bird makes for his own territory adopting the stretch posture until he is safely past the danger. As he runs past he shows no inclination to attack the owner but rather the opposite. If the owner makes a sudden movement towards him he starts away and the stretch posture is exaggerated. On the other hand a bird which is merely frightened, for instance at a human intruder or a rabbit or even another tern, does not adopt the stretch but the usual alarm posture with the bill horizontal and neck stretched. One must therefore seek some other feature which is common to all the situations where the stretch occurs but which is absent when the alarm posture occurs. This common factor seems to be that the tern is close to the object which is frightening it. This may be because, as in the example cited, the bird has to pass close to another in order to reach his territory; it may be because it has to approach

another in order to get a fish, or to mount or to be mounted; it may be that the reason which caused it to approach close to the other has suddenly disappeared as happened when a male brings a fish to his mate and at once does a stretch after she has taken it from him. But in those situations where the alarm posture occurs the fear is not counterbalanced by anything which draws the tern close to the frightening object. Only when there is a conflict of fear with something else does the bird stretch.

There is one posture more whose motivation I want to discuss. This is the bent, which is the male's reaction to the alighting of the female and does not occur in fights. However one sees sometimes that the male reacts to another bird with the bent and then this grades into the crouch if the other doesn't react suitably and may finally end in an attack. The fact that the crouch and bent can grade into one another in this situation and that they have certain important elements in common suggested to me the relation between them. Some of the differences between them were also highly suggestive. The orientation of the two towards the provoking birds is very different. The crouching bird faces precisely towards the other and displays his black cap in this way. The bent bird, however, takes a number of precautions not to show his black cap to the female. Firstly he tends to turn his body in such a way that she lands or approaches to one side rather than directly in front of him. Secondly he tends to bend his head and neck sideways away from her and thirdly he actually rotates the head about its long axis so that the black cap is turned further from her. This last effect I call Tilting and is also very conspicuous in birds in the stretch. Thus comparing these two postures we see that in the one which is used in hostile situations the male directs his cap towards an opponent while in the greeting he prevents her seeing it. Further observations confirmed what will already have been guessed that the black cap appears to frighten other terns. Sometimes a female moved around a male when he was so engrossed in his display that he did not change his position. On catching sight of his cap she at once moved farther away from him but was reassured when he once more tilted it away from her. If there were a predisposition in some ancestor of the Arctic tern to perform a hostile action like the crouch towards females who visited him during pair formation (and there are now sufficient reasons for this view) one might expect that those terns would pair most easily who developed various ways of avoiding frightening their visitors. I believe that it is such a modification of the crouch which has brought it into the form of the bent today. Why the modifications should have been of just the kind they are is another and a more difficult question.

So far I have suggested nothing about the motivation of the serial displays. There is very little doubt that the form, and therefore presumably the motivation, of the stretch and bent roles in the serial pass is similar to when they occur on the ground. Apart from this I have seen little convincing evidence

about their motivation. One can recognise some elements of attack and escape but the display in fact very rarely leads to either while its main occurrence is between potential or actual partners so that I suppose sexual tendency must be important even though one cannot identify any specifically sexual elements in the movements.

This discussion of the motivation of courtship and threat displays shows the sort of difficulties which arise and the sorts of ways they can sometimes be overcome. A further valuable source of evidence comes from related species. At the moment the behaviour of other species of terns is under investigation in Holland, America and elsewhere. The first results of these studies are beginning to be published and starts are being made on more and more species. According to my observations the black cap in the Arctic tern seems to be a threat structure. Since a black cap is found very widely among terns one might expect that all these species also had some threat posture which displayed the cap towards rivals. In the last year I have been informed from published work on the Caspian tern and as yet unpublished observations on the Sandwich tern that it seems that both may have such a posture. My personal observations, though brief, on the Common, Roseate and Sandwich terns which are taxonomically farther and farther removed ^{independently} from the Arctic have shown me the value of such comparisons. One can remark in parentheses that the opportunities in the Farnes for watching these four species of terns, to say nothing of three species of the related gulls, must be unique.

Nest building in the Arctic terns is not a very elaborate business. Unlike the gulls there is no collecting of beakfuls of material from a distinct spot far from the nest. Rather there accumulate on the nest rim all the pieces of shell and stick in the vicinity of the scrape. Each time a tern walks away from its nest-scrape it usually picks up such objects and deposits them to one side of its body. Each time a shell is carried it moves a few inches closer towards the nest so that by the time the eggs hatch quite a number of objects may have accumulated. The hollow of the nest is made by the scraping activity like that used by the male after greeting. It seems that as a rule one of the scrapes which the male makes in this way is finally used by the female to lay her eggs in. As a scraping bird tends to select a slight hollow to perform in the birds with territories on rock generally have their eggs in little depressions which are at once flooded and the eggs drowned by a shower of rain.

The causation of scraping was investigated and I found by making experiments with wooden eggs that the scraping which follows the greeting of the mate is a different kind from that which one sees the parent doing after the young are hatched. This latter kind of scraping is an expression of frustrated broadness while during greeting it is frustrated sexual activity. (A tendency is said to be frustrated if it is arcused by the appropriate stimuli but for one reason or another cannot express

itself normally.) In other words two kinds of displacement scraping were studied. Scraping which is not some kind of displacement activity hardly ever occurs in ^{Arctic} terns though it ~~it~~ certainly did so in the ancestors and still does in the related gulls as well as in some groups of terns. This shows once again how the motivation of behaviour may change in evolution.

The process of laying an egg was watched a few times and I was specially interested to see how the brooding behaviour of the parents developed. The male at first was very reluctant to sit and concentrated on feeding the female. Later both alternated in brooding the eggs. I have not yet worked out fully the proportion of time spent brooding by each sex at the different nests. In one pair out of 322 observations made throughout the incubation period at intervals of not less than 10 minutes the male was sitting in 69%. But in the first ten days after hatching he sat only 39% (177 observations). As most of the observations on which these figures are based were made between 5 a.m. and 1 p.m. it is not possible to conclude that 69% reflects the real contribution of the male towards brooding. It might be that my data are the result of a slight tendency for the male to brood more in the mornings and the female more in the afternoons. At any rate it is possible to test for regularities though this is not yet completed.

In 1954 all the nests in a certain area of sand were kept under observation to see when the clutch was complete and to study the success in rearing young. Some of the nests were washed away by a spring tide so there were a number of relayings but these could not be distinguished from first layings as the identity of most of the pairs was not known. 90 clutches were completed in all and showed the following distribution of clutch sizes:

| | |
|--------|----|
| 1 egg | 27 |
| 2 eggs | 62 |
| 3 eggs | 1 |

with a mean value of 1.7 eggs per clutch. This figure was the same as the one arrived at the previous year by a less exact method. The Common tern lays a rather larger clutch of two or three eggs. A few percent of the total number of nests in the whole Inner Farne tern colony contained three eggs and some of these were genuine Arctics. I could distinguish them only by watching to see the species of the parents. There were even some Arctic nests with four eggs but in no case did I know the history of the clutch. In none of the cases I had under observation could I be sure that more than one female had laid in a certain nest but from the general laxity of territorial restrictions, ~~as~~ especially after the spring tide had swept over much of the beach, I should not be surprised if such a thing sometimes happened. In 31 nests the incubation period of the eggs was

known with an accuracy of $\pm \frac{1}{2}$ day. It was about 224 days for the first egg and a shade longer for the second. The difference for the two eggs is probably significant and must reflect the relative inefficiency of the first day or two of incubation, as the eggs are usually laid at an interval of two days and incubation starts with the first.

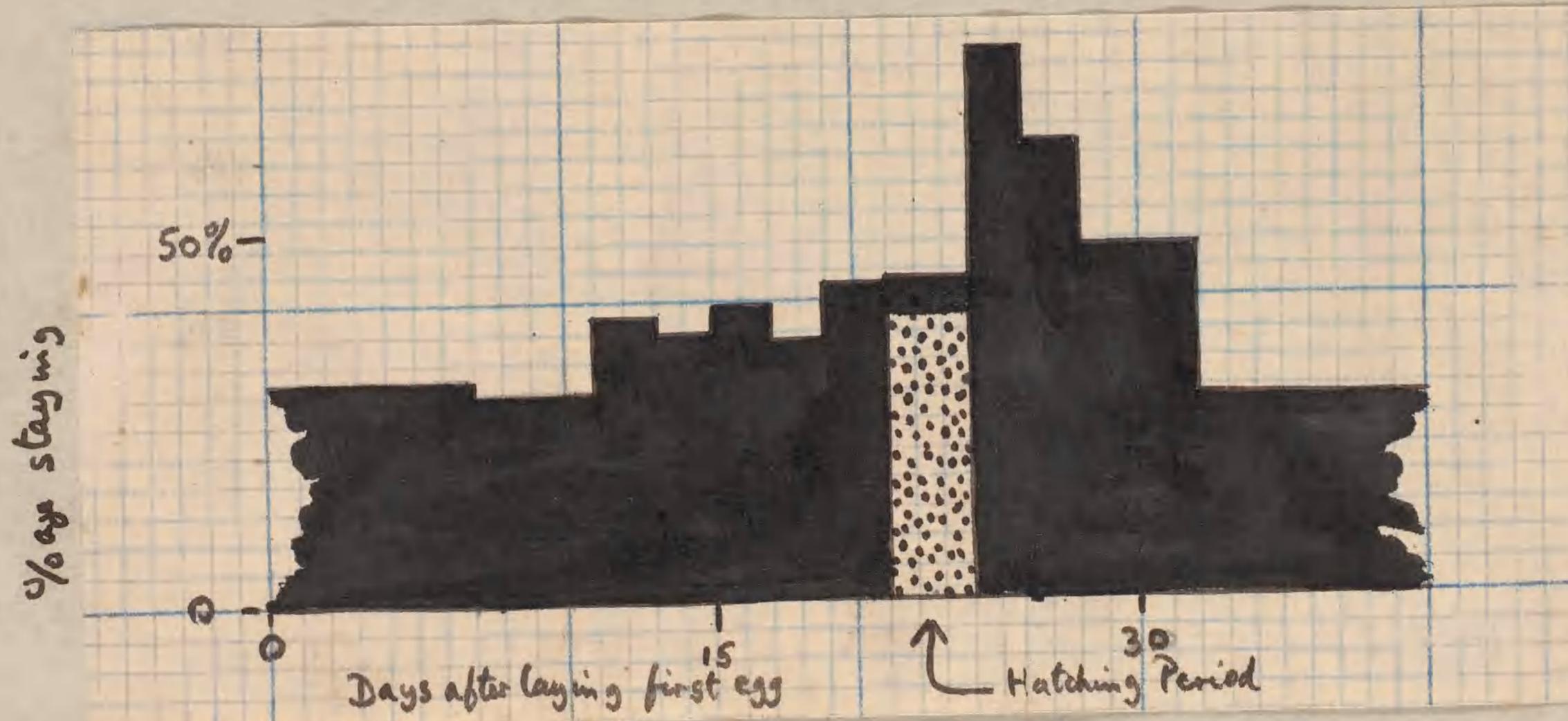
The knowledge of laying dates in the different nests was used for something else. It is well known that the terns will swoop at and even peck intruders who walk about in the colony, especially when the eggs are hatching. By offering a standard "predator stimulus" and by counting the number of swoops made by the brooding bird of a particular nest I could measure fluctuations in the terns' aggressiveness towards predators. In this way one could see how far the behaviour corroborated expectation. As might be expected it was necessary to be sure of the identity of the brooder as the two parents often reacted quite differently. There was no indication that in all pairs one sex swooped more than the other. The variation in response of one bird between one day and the next was rather slight which suggested that it was not subject to much short term fluctuations depending, for example, on whether the bird had just taken over brooding from its mate. This was just as well because only the minimum amount of disturbance was possible. In fact there were no desertions as a result of the experiments. The behaviour of 5 pairs was studied and in each I could tell which bird was male and which female. The completeness of the record of attacks varied from pair to pair and it was clear that there was a very great variability between different pairs. Some pairs never attacked at all, in others only one of the parents ever attacked. But if this variation is ignored and all the data are put together it is possible to calculate the average number of attacks for each of the 5-day periods from the date the first egg was laid. I have used only the data from periods Day 6 to Day 30 because outside this span all the observations were based at a single nest. The following table shows the average number of attacks in each of the 5-day periods.

| Day | 6-10 | 11-15 | 16-20 | 21-25 | 26-30 |
|-----------------------------|------|-------|-------|-------|-------|
| Total no. of swoops | 15 | 31 | 37 | 224 | 95 |
| No. of tests | 11 | 15 | 16 | 41 | 31 |
| Mean no. of swoops per test | 1.36 | 2.07 | 2.31 | 5.46 | 3.06 |

Thus the expected increase in attacks was found in that period when the young hatched. There also appears to be an actual increase from the beginning of incubation up to the time of hatching. This might have occurred by chance and it is necessary to apply statistical tests to find if this trend is not merely due

to chance. It will probably be necessary to collect further observations to refute this possibility.

Since the broodiness of birds also increases towards the time of hatching I was interested in the relation between this and swooping. In the first place I had to try and see if I could demonstrate such an increase in broodiness. Several ways were attempted but the following one showed most clearly the effect. During the time of incubation occasional panics, five or six during a morning, were still disturbing the colony and each one offered a choice, so to speak, to each brooding bird whether it should leave its nest or not. Sometimes a bird stayed and sometimes it left. One would expect that the chances of staying increased the more broody the bird was. I made notes of the choices at each panic for several nests which were often at different stages of incubation. Then at the end I collected the data from all the nests for each day of the incubation period. For instance putting together all the nests there were 51 choices made by birds on the 13th day of incubation. In only 17 of them (33%) had the brooder stayed on the nest. To make the percentage calculated more valid I grouped the days in pairs (or longer periods when the number of observations was few). The following histogram shows that the percentage does in fact increase slightly towards hatching and is specially high just after the young hatch. A test of the data in the first and second halves of incubation suggest that ~~then~~ there is a real increase even before the eggs begin to chip.



Having established that there is a general increase in both the number of swooping attacks and in the broodiness during incubation I must next find if it is possible to correlate variation in one with variation in the other. For example is it true that the birds which breed most ~~steadfastly~~ are those which attack most vigorously? I have the necessary data but the analysis is not yet finished.

Another problem I have started on is whether there is one kind of aggressiveness for predators and another for other terns. To do this it is necessary to study very carefully the distance from the nest which trespassing terns were able to reach before releasing various threat postures in the sitting bird and how close they could come before they were attacked. In one nest where this was done on more than a preliminary scale enough data were collected to show some effects, such as that the male would react at a greater distance to intruders than the female. It was also found that the reaction distance of a bird was much greater if it were standing by the eggs than if it were sitting on the nest. Actual brooding seems to inhibit aggressiveness, not only in preventing attacks but also in preventing the bird uttering aggressive calls and threat postures. If this is true, and it was not unexpected, the correlation between broodiness and aggressiveness is not complete. While there may be a general tendency for the two to fluctuate together over a matter of days, over a few minutes they may be inversely correlated. This indicates one of the complications which may upset the simple picture and it is just such complications which cause the great variability in results and make the establishing of true relationships such a long and difficult task.

One of the disadvantages of field studies is the shortness of the season. As the whole colony passes first into the courtship phase and then to egg laying and finally to rearing young the problems which one can tackle also succeed one another. One ~~if~~ cannot concentrate on one aspect of the reproductive behaviour for the whole season. After a few tentative beginnings at analysis of the relation between aggressiveness and broodiness the last eggs are hatched and one is swept on into the relations between parents and young.

The feeding of the young was of particular interest as it was evidently quite difficult in 1953 for the parents to find fish and many of the young on the beach died. There was intense food competition between the young and the later hatched ones were robbed again and again by their companions until they died of starvation. 1954 was a good season and there was hardly any mortality at all. In 1953 the end of the season was mainly devoted to watching one chick and his brother and their behaviour with one another, with their parents and with other adults and young. Curiously enough there were three birds who fed the chicks. The third showed an interest in them from the earliest days and was probably the same individual who had

continually courted the female while she was brooding and had been repeatedly attacked by her husband. However a few days after hatching the ^{extra bird} showed signs of wanting to brood the chicks and even did so. He started feeding them and gradually took more and more part until his contribution was as great as the two parents ~~together~~ together. The following table shows the percentage of feedings I witnessed by the three birds in the first and second twenty days after hatching.

| | Total no. of feedings observed | Contributions: | | |
|----------------|-----------------------------------|----------------|--------|------------|
| | | Male | Female | Extra bird |
| First 20 days | 84 | 49% | 37% | 14% |
| Second 20 days | 70 | 33% | 19% | 48% |

In another nest in 1953 I saw that a third bird was playing a part in incubation. He first appeared to take a special interest in the brooding female some days after she laid. At first he courted her and was driven off but after a time he was even allowed to relieve her on the eggs. The husband male first drove him off whenever he found the stranger at the nest but later, I think, also accepted him. In 1954 I kept a look-out for the possibility of "triple parents". In two nests it appeared to be developing but one nest was accidentally destroyed and the other hatched and the young moved out of my range of vision. In both cases the additional bird behaved like a male. In a great many other nests, perhaps nearly a half, there were additional birds who behaved as unmated males and courted the brooding females with great intensity and even tried to mount them. In this they were sometimes successful but the female would always rise from the nest and try and get rid of them. At several nests I was able to identify these extra males and found that it was always the same bird who would be pestering the brooding female day after day. Although they were unable to develop a normal relationship to the brooding female they showed a clear preference for one particular bird and showed their feelings for her as far as she would allow them.

In 1955 the facilities on the Farne were also used to study the growth rate of the tarsus in the Arctic and Common terns. The actual means of measuring the length is immaterial except that it was constant in all my measurements of all the young. The tarsus length of young of known age was measured in as many young as possible but it was rarely feasible, especially in the Common tern to get more than a few values (sometimes only one) for each day of age. The figure below shows that although the mean is greater in the Common tern from the day of hatching onward, the actual measurements overlap at first in the two species. Only when the young are over a week old do the measurements effectively cease to overlap. Thus even if a standard method of measuring could be described and was carried

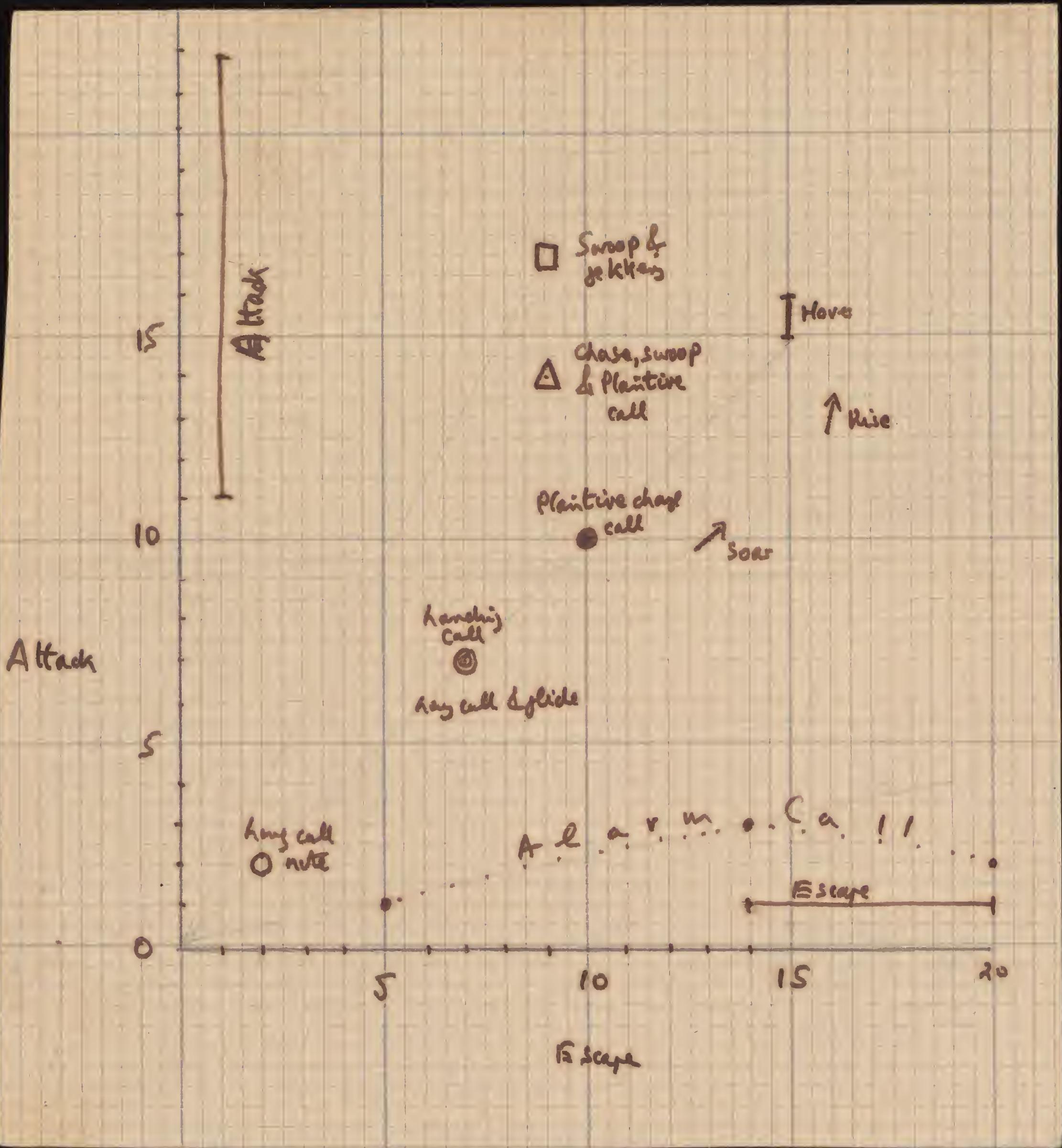
out sufficiently carefully it would still be dangerous to try and distinguish young of the two species, e.g. for ringing, until they were about ten days old. In their juvenile plumage I found I could distinguish ^{the two species} as the Common terns were usually a lighter brown but the variability is so great, at any rate in the Arctics, that this method would probably not be completely successful even after considerable practice.

To return to the development of the young I was specially interested to see how they first began to fly. I was able to see not only this but also how they learnt to fish. The favourable topography of the colony of the sand on the Inner Farne allowed me to survey both the breeding area and at the same time the Kettle over which the young birds flew a few days after they had first succeeded in fluttering off the ground. Without any instruction by the adults the young begin to swoop to the water surface and pick up small objects floating there. These usually appear to be pieces of seaweed and after carrying them a few seconds they would drop them only to swoop for them once again. At this time they return to the approximate area of the nest to be fed by their parents but they become less and less tied to this area and spend more and more time on the preening places with the adults. Here they continue to be fed by what I believe to be still their parents. I have seen a presumed parent with a fish flying slowly up and down the whole length of the colony calling repeatedly as they do whenever carrying a fish. Only after nearly two complete traverses of the colony did I see a young bird on the preening rocks suddenly food-beg wildly and at once the parent swooped down and fed it without hesitation. Young will beg from any adult with a fish and adults with a fish are inclined to feed any young who begs, but there is always some hesitation except when it is the right parent and the right young.

During August more and more young start to fly and desert the breeding area for the rocks close to the water. The total number of adult terns has also decreased but I found it difficult to get any exact impression about how soon the total adult population begins to drop. The build-up at the beginning of the season is easier to see because it takes place so quickly but a couple of weeks after the first arrival so many are about that I can't recognise any further increases in their number. However at the end of May or beginning of June (it was 6 June in 1953) the first one-year old birds are seen about. Only a few individuals are seen and they may join in a little of the courtship but usually stand about looking as if they don't quite know why they are there. They seem to disappear by the end of June. Two-year olds also arrive later than the main body of adults and take more part in the courtship than the one-year olds and may even mate and rear young. These two-year olds become a more conspicuous fraction of the birds on the colony area as the adults rear their young and move away from the nesting places. They are among the last to desert the colony area and up to the end some behave like unmated birds contemplating

starting the whole business of rearing a family. The ageing of the birds seen is supposed from the plumage and based for the most part on museum studies. But if one sees a bird in a so-called one-year old plumage visiting the breeding area one can suppose either that his migratory instinct has matured more rapidly than the development of his plumage or that his plumage has lagged behind. There is no obvious reason to suppose the plumage is a more accurate indicator of his actual age than his tendency to migrate. This question has already been considered by Austin on the Common tern in America but it would be interesting to compare his results with what may be gleaned in a far shorter study of the Arctic terns of the Farnes where so many individuals have been ringed before and since the war. In 1954 for the first time I saw one of the birds which I had colour ringed as a chick two years before. Next year he may be breeding.

In 1954 the actual departure of the terns was watched a number of times. It took place in the evenings from about 4 p.m. until it was too dark to see any more. Small parties collect, often as a result of panics, and these circle higher and higher drifting away on the wind. Young and adults were usually mixed together. Every now and then they might form themselves into loosely integrated flocks which would fly all together in one direction for some seconds, but they would almost at once disperse and perhaps descend earthward again to resettle on the rocks which they had left. Most of the flocks did not return to the ground once they had reached a good height but tended to fly in a more and more organised way, not closely packed but flying steadily in a manner and at a height totally unlike anything I had seen in the whole of 2 season's observations on terns at the breeding grounds. Then they grew to small specks in the distance their formation reminded one of high-flying lapwings. By following these flocks we found that they were not flying steadily in one direction. They might travel for several minutes north-east and then one wing of the group would break away in a more southerly direction and the others would soon follow. Then once again the flock would alter course until they were all flying west. We watched a number of flocks until we lost them to sight but found no tendency that they went off even in a predominantly southerly (or any other) direction. But it was difficult to follow the flocks owing to their great height. We sometimes picked them up flying over the island so high that one could not see them with the eye and even with glasses they appeared only as points of silver flashing in the evening sun. Each time the birds beat their wings, the whole flock gave the impression of a little constellation of stars passing to their winter quarters.



15

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13
Calls in Arctic Tern.

Fear call, a shrill "keer". Rare. Heard when adult handled and occasionally during a fight on the ground when one bird has hold of another who is trying to get free.

→ Alarm call, low intensity, single "jek". Nervous bird in any ^{Anxious} ~~any~~ situation. Doesn't seem to grade into the chatter.

LCN? Alarm call, higher intensity, "kair" or "keyair", like last but probably more aggressive. The chief call heard when you walk through a tern colony as the birds hang overhead.

Clash call, a loud sudden "kyow" by a swooping bird at the bottom of the swoop as he comes closest to striking a predator, by two birds in an upward flutter. Usually precede by ~~chatter~~ when swooping at an intruder. Sometimes becomes "keyair" if the attacker loses heart at the last moment.

Chatter, "tikitikitikit...", during downward swoop of an attack, also by a bird on ground, e.g. brooding, as another or a rabbit comes near.

ky₁ "keeyer". A colourless call often heard from birds fishing, flying to or from the colony, etc. At moments of greater excitement turns into ky₂ or ky₃.

ky₂ "tikiteeyer tikiteeyer teeyer teeyer tikiteeyer....."

The commonest intraspecific aggressive call. Accompanies threatening matches on the ground and aerial fights too. The typical call of a bird with a fish in the air or on the ground, though it goes into ky₃ when he attracts or tries to attract a female. Typically the first reaction of a bird on the ground to a flying bird. The call with which an unmated male advertises himself as he flies to and from over the colony. It goes into ky₃ if another condescends to make a "fish flight" with him.

ky₃ "Keeyor yor yor keeyor keeyor yoryoryor....." ky₂ grades

into this call as a mate approaches either on the ground or in the air. It accompanies the bent posture and is often continued to accompany the scraping which follows greeting. At nest relief this call indicates broodiness.

Also f. begging, copulation call (a form of ky₂ or ky₃) and a couple of other calls of doubtful distinctiveness.

On the basis of the Arctic's calls I looked at the repertoire of the common, roseate, Sandwich, Caspian and black terns based on my own obs supplemented by the people who know about them. Also a complicated correspondence with Bergman about the Caspian where the two letters "r" and "a" just about exhaust this species' alphabet but not its inflection.

Reviewing these species one can make out the following list of characteristics of the various calls:

Food begging. Regular repetition of a single ^{non. metallic} syllable. Frequency varies from sp. to sp. Pre-feeding and pre-cop.

Weak alarm call. Single monosyllable, often harsh.

Stronger alarm call. Relatively longer than last. Given towards intruders near the nest.

Chatter. Rapid repetition of a single ^{metallic} syllable. Accompanies aerial swoops and ground hostility.

Fish call. A single polysyllabic call often occurring singly, but several calls may be strung together though usually in a rather irregular way. A bird suddenly starts to utter this call when he catches a fish which he intends to take to his mate or chick, and keeps it up till the fish is delivered.

Soft Call. A soft growly call consisting of the repetition of a fairly simple phrase. The growling may go on for many seconds. Especially at nest relief, also sometimes in greeting or scraping.

Clash call. A single loud call, not metallic. Accompanies fighting or the lowest point of a swoop.

One of the most interesting points in this survey of these calls ~~is~~ concerns the Fish call. In the Caspian this is different from the aggressive call and B. denies any aggressive content. This fits very much with my impression of the fish call on the Sandwich and Roseate. In the common and Arctic the fish call is indistinguishable from the normal aggressive call. N.B. The fish call of the Arctic is ~~ky~~ ^{fish call because} ~~ky~~ the call they make ~~it~~ with a fish.

Thus Caspian, Sandwich and roseate have a fish call which is not commonly used in fights and when threatening use the chatter (= gekkering); while Arctic and common rarely use the chatter in fights but ~~never~~ ^{instead} ~~ever~~ the fish call. The black tern has a fish call and a chatter but which is used in fights I don't know. These facts suggest that there has certainly been a shift in motivation of the calls in the different species. Whether there is no aggression ^{at all} in the fish call of the Sandwich etc ~~now~~ I don't know but if it were as conspicuous as in the Arctic it couldn't be missed.